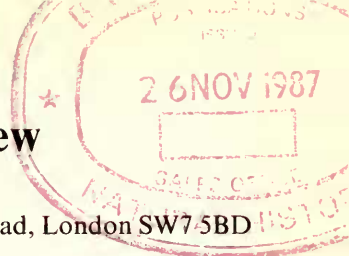


The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review

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Introduction

The main objectives of this paper are three-fold. First, to revise and review, at the generic level, a major group of west African taxa often referred to as the Pelmatochromines since all were once classified in the genus *Pelmatochromis*. Second, to determine whether these genera are closely related phylogenetically, and third, to examine their intrafamilial relationships. It is hoped that the information gained in this analysis will be a contribution towards any ultimate investigation of intrafamilial phylogeny in the Cichlidae as a whole.

The term 'pelmatochromine' used here has no implied or established taxonomic or phyletic implications. It is employed simply as a convenient reference to the various supraspecific groups recognised by Thys van den Audenaerde (1968*a*) in his revision of the speciose west African genus *Pelmatochromis* Steindachner, 1894.

Thys'¹ paper marks an important change in our taxonomic understanding of these fishes, especially since it is the first attempt to break down Regan's (1922) manifestly polyphyletic *Pelmatochromis* generic concept into a number of monophyletic lineages.

¹Following current convention, Dr Thys van den Audenaerde's name will be abbreviated to Thys in all future references to his work cited in the body of the text.

Although Thys retained his various lineages within a nominal *Pelmatochromis*, he did suggest the recognition of three subgenera (*Pelmatochromis*, *Chromidotilapia* Blgr. 1898, and *Pelvicachromis* Thys, 1968a). He also included, as a subgenus of *Pelmatochromis*, Pellegrin's (1904) *Nanochromis* which Regan (1922) had regarded as generically distinct from that genus but closely related to it. In addition to these four subgeneric groups, Thys included in *Pelmatochromis*, but as taxa *incertae sedis* with regard to their subgeneric placement, a number of species treated as members of *Pelmatochromis* by Regan (1922), together with others which had been described since 1922 (see Thys, 1968a, and pp. 154 & 160).

Later in the same year Thys (1968b) placed the nominate subgenus *Pelmatochromis* (*Pelmatochromis*) in *Tilapia* Smith, a move contested by Trewavas (1973) who resurrected the taxon as a genus, and thus by implication raised the other *Pelmatochromis* subgenera to full generic rank. Trewavas (*op.cit.*) also included in *Pelmatochromis* one of the species (*P. ocellifer* Blgr, 1899; but see Trewavas *op.cit.*) which Thys (1968a) had treated as being of uncertain subgeneric affinity, and resurrected another species (*P. nigrofasciatus* [Pellegrin, 1900]) which he had synonymised with *P. ocellifer* Blgr, 1899.

The following year Trewavas (1974) explicitly returned the subgenus *Chromidotilapia* to its former generic rank, thus, again by implication, recognising the subgenera *Pelvicachromis* and *Nanochromis* as genera.

Of the pelmatochromine taxa which Thys (1968a) treated as of uncertain infra-generic relationships, *Pelmatochromis ruweti* Poll & Thys (1965) has been placed in *Tilapia* (Thys, 1968a), *P. congicus* Blgr (1897) has become the monotypic taxon *Pterochromis* Trewavas (1973), *P. ansorgii* was made the type species of the genus *Thysia* Loiselle & Welcomme (1972), *P. cerasogaster* (Blgr, 1899) was included in *Hemichromis* Peters by Loiselle (1979), as was *P. exul* Trewavas (1933) by Trewavas (1973), and *P. thomasi* (Blgr, 1915) has become the type species of the currently monotypic genus *Anomalochromis* Greenwood (1985b).

Since *Pterochromis* and *Thysia* would, at least superficially, seem to qualify for inclusion in any review of the pelmatochromines, both are considered below. There seems no doubt that *Pelmatochromis ruweti* is indeed a species of *Tilapia* (see Trewavas, 1983), and that *Hemichromis* and *Anomalochromis* are not closely associated, phylogenetically, with the pelmatochromines (see Greenwood, 1985a & b; also p. 195). Thus, little more will be said about the two latter taxa except in a general context.

The pelmatochromines, as here restricted, are a moderately large group comprising some 35 species, to which more will undoubtedly be added when the various genera are subject to revisions at the species level. Geographically speaking, the assemblage is a west African one whose range extends from Senegal in the north to the Zaire river and several of its tributaries in the south. Within that area some of the constituent genera have relatively circumscribed distributions, and many of the species would appear to occupy even more localised areas. No pelmatochromines occur in any of the African Great Lakes (see below) and none has been recorded in other habitats within what is considered to be eastern Africa (i.e. east of longitude 29°E). Within west Africa no pelmatochromines have been recorded outside the region bounded by latitudes 18°N and 9°S. The supposedly unique pelmatochromine representative in east Africa, *Pelmatochromis exul* Trewavas from Lake Turkana, is now known to be based on the misidentification of three small *Hemichromis bimaculatus* specimens (Trewavas, 1973). In itself that corrected record is of interest since it represents the most easterly occurrence of *H. bimaculatus*, a species belonging to an otherwise essentially west African genus (see Loiselle, 1979; Greenwood, 1985a).

Most of the pelmatochromine species occupy fluvial habitats, with some seemingly restricted to fast flowing, even torrential waters, as is the case with many *Nanochromis* species (see Roberts & Stewart, 1976; Stewart & Roberts, 1984).

In many respects the pelmatochromines are the ecological counterparts of several haplochromine taxa (*sensu* Greenwood, 1980) in east Africa, particularly with regard to species of the genera *Astatotilapia*, *Thoracochromis*, *Ctenochromis* and *Orthochromis* (Greenwood, 1979). It is this apparent haplochromine-pelmatochromine equivalence which, in part, aroused my interest in the pelmatochromines, particularly from the viewpoint of possible phyletic relationships between either individual genera or the two groups as a whole.

Thys' (1968a) analysis of the pelmatochromines was based on what are now called orthodox or evolutionary taxonomic lines. A cladistic (or Hennigian) approach is used here, both to test the hypothesis of intragroup relationships put forward by Thys (his subgenera) and to erect an hypothesis of interrelationships amongst those lineages, a problem only touched upon by Thys (1968a; fig. 17). Using the same methodology, I shall also attempt to establish the wider, intrafamilial relationships of these various lineages, especially to test Thys' (1968b) hypothesis that the phyletic relationship of at least some pelmatochromines lies with the genus *Tilapia* (*sensu* Trewavas, 1983).

Thys' inclusion of two *Pelmatochromis* (*Pelmatochromis*) species in *Tilapia* was strongly contested by Trewavas (1973), and I would support her views, albeit from a different standpoint. That difference raises questions about the validity, in phylogenetic arguments, of the characters used in previous discussions, and questions the current definition of the genus *Tilapia* itself and of the tilapiines *sensu* Trewavas (1983) as a whole, a lineage which includes certain pelmatochromine genera.

Materials and methods

Materials. The entire spirit collection of pelmatochromine species in the British Museum (Natural History) was examined. Those specimens from which new skeletal preparations were made are listed separately, together with those used for dissection; often a dissected specimen was later prepared as a skeleton.

Dissections used for previous studies (see Greenwood, 1978; 1983; 1985a & b and 1986), and named in those papers, are not detailed here.

Most of the British Museum (Natural History) collection of cichlid skeletal material (both dry and alizarin preparations) was examined or has recently been examined (see Greenwood, 1985a and 1986). For extra-familial out-group comparisons, the Museum's skeleton collections of the Serranidae, Centropomidae, Sparidae, Labridae and Pomacentridae was examined (see Greenwood, 1976; 1985a), and other anatomical data were derived from various specimens detailed in Greenwood (1985a & b and 1986).

All the specimens mentioned below are listed under the generic names in use before this revision, that is, following Thys (1968a) and Trewavas (1973 and 1974).

Additional material examined for superficial characteristics is as follows:

Museum of Comparative Zoology, Harvard University: *Nanochromis splendens*, holotype (MCZ 50476) and paratype (MCZ 50311); *N. parilius* holotype (MCZ 50474) and 8 paratypes (MCZ 50340); *N. consortius*, holotype (MCZ 50551); *N. minor*, paratype (MCZ 50310); *Pelmatochromis buettikoferi* (MCZ 35465, 60 & 38 mm SL); *Chromidotilapia guntheri* (MCZ 48071; ca 70 mm SL); *Chr.cf. guntheri* (MCZ 48135, ca 60 & 45 mm SL, and MCZ 32524, ca 70 mm SL). *Nanochromis longirostris* (MCZ 35398; 10 specimens 45–75 mm SL, and MCZ 35389, one specimen ca 60 mm SL). *Thysia ansorgii* (MCZ 48070, one specimen ca 54 mm SL).

Musée de l'Afrique Centrale, Tervuren: *Pelmatochromis nigrofasciatus* (det. E. Trewavas; registered as *P. ocellifer*), 3 specimens (from MCA 118090–99); *Pelmatochromis nigrofasciatus* 2 specimens (MCA 52454–55); *Nanochromis cavalliensis*, holotype (MCA 168574), and 4 paratypes (MCA 1963–471).

California Academy of Sciences: *Nanochromis robertsi*, holotype (SU 63143) and 2 paratypes (SU 67173). British Museum (Natural History): *Myaka myaka* (1973.5.14:717–23). *Konia dikume* (1978.5.14:643–59); *K. eisentrauti* (1961.10.18:11–14). *Pungu maclareni* (1973.7.18:137–140). *Stomatapia mariae* (1973.5.14:984–988); *S. mongo* (1971.10.20:24–33).

Dissections, partial dissections, and osteological preparations (see above) involved the following specimens (all from BM [NH] collections unless indicated otherwise): *Chromidotilapia batesii* (1912.6.29:4; skeleton), *Chr. finleyi* (1973.5.14:544; dissection and skeleton), *Chr. guntheri* (1973.5.14:615–625 and 1934.8.31:179–188, one specimen of each: dissection and skeleton), *Chr. kingsleyae* (1867.5.3:2; 1912.4.1:526 and 1908.5.30:186; both skeletons). *Iranocichla hormuzensis* (paratypes, 1981.1.12:1–2; partial dissection of one). *Nanochromis cavalliensis* (holotype, MAC 168574; partial dissection of pharyngeal region); *N. parilius* (paratypes, MCZ 50475; 4 specimens as alizarin preparations, and BMNH 1977.1.11:33–34, paratype; one specimen as an alizarin preparation and partial dissection); *N. nudiceps* (1963.10.22:9, and one unregistered specimen, from below Stanley Pool, collected by Mr Owen Clark; both partial dissections). *Oreochromis macrochir* (J. L. B. Smith Institute, RUSI 22134; dissection); *O. mossambicus* (RUSI 19290; dissection); *O.*

niloticus (1981.2.17:601–620; one specimen partially dissected); *Pelmatochromis buettikoferi* (syntype, 1911.5.31:47; a skeleton, and 1981.6.19:103 and 1983.1.25:38; dissected and skeletonised); *P. longirostris* (1903.7.28:77–88; one specimen, an alizarin preparation, another dissected and skeletonised), *Pelvicachromis humilis* (1915.4.13:441; dissected and skeletonised, and 1972.3.16:8–10; one specimen dissected and skeletonised); *P. kribensis* (syntype, 1912.6.29:28; skeleton); *P. pulcher* (syntypes, 1901.1.28:13–20; one specimen dissected, and one already a skeleton; 1908.12.9:68; a skeleton); *P. subocellatus* (1888.12.13:8–10; one specimen skeletonised). *Thysia ansorgii* (1977.11.8:436–455; five specimens dissected and some skeletonised). *Tilapia busumana* (1934.8.31:189–199; one specimen skeletonised, and 1942.12.30:38–42; one specimen dissected and skeletonised); *T. ruweti* (1969.3.28:1–6; one specimen dissected and skeletonised; another specimen, ex Okavango Swamps, Botswana, unregistered, treated similarly); *T. sparrmanii* (1907.3.15:45–47; one specimen dissected and skeletonised, and RUSI 23538, dissected). *T. zillii* (1973.3.27:7–8; one specimen dissected). *Tristramella simonis* (1949.9.16:399–444; one specimen dissected and skeletonised).

A list of the *Tilapia*, *Oreochromis* and *Sarotherodon* species examined (and some partially dissected) in connection with the nature of the pharyngeal teeth and the arrangement of the pharyngeal bones (see pp. 148 & 198), and of the non-tilapiine taxa also examined is available in the Fish Section of this Museum.

Methods. The methodology employed has already been discussed in relation to that of Thys (1968*a*) and Trewavas (1973, 1974); no further comment is required (see p. 141 above).

Since the species-level taxonomy of the pelmatochromines, especially the genera *Pelvicachromis* and *Chromidotilapia*, is in a rather unsatisfactory state at present, I have concentrated my attentions on the type-species of the various genera. This is particularly so with regard to anatomical data and, where information is available, on the natural history of the species. Nevertheless, other species have not been neglected (where material permitted) and, as far as possible, are included when intergeneric comparisons are made. Likewise, particular attention has been paid to the correct specific identification of the specimens used. Whenever sample size allowed, these have been taken from amongst the syntypes of a species.

A review of Thys' supraspecific pelmatochromine taxa

As Thys (1968*a*) recognised, the pelmatochromines can be divided into two groups on the basis of at least one feature, namely the nature of the pharyngeal roof immediately anterior to the upper pharyngeal bones.

In one group, to which the majority of taxa belong, this tissue is organised into a distinct, visor-like pad projecting downwards and forwards for a short distance in front of and medial to the epibranchial of the first gill-arch, and is clearly circumscribed from the roof of the bucco-pharyngeal cavity by a distinct transverse groove (see Trewavas, 1974:389–391; Greenwood, 1983: 265–267). Associated with the presence of this pad (but probably not in a functional sense, see Trewavas, 1974; Greenwood, 1983) is an absence of microbranchiospines on any gill-arch.

The second group has no visor-like pad. The comparable area of the bucco-pharynx (as in the majority of cichlids) is merely a little more pachydermatous than the surrounding tissues. In this group, too, as in the majority of cichlids, microbranchiospines are present on the lateral aspects of gill-arches 2–4. The absence of a hanging pad, and the presence of microbranchiospines are taken to be the plesiomorphic condition in cichlids.

As was noted above (p. 140) Thys' supraspecific groups, some a little modified, are now recognised as genera, and some of his taxa, unallocated to a group, have recently been placed in newly described genera. It is as genera that they will be reviewed below.

I Pelmatochromines with microbranchiospines but without a pharyngeal hanging pad

PELMATOCHROMIS Steindachner, 1894

TYPE SPECIES: *Pelmatochromis buettikoferi* Steindachner, 1894 (subsequent designation by Regan, 1922:252).

SYNONYMY. *Pelmatochromis* (part): Steindachner, 1894 (the species *buettikoferi* only); Pellegrin, 1904 (the species *buettikoferi* [with which *ocellifer* was synonymised] and *nigrofasciatus*); Boulenger, 1915 & 1916 (the species *buettikoferi*, *ocellifer*, and *nigrofasciatus* [in part]); Regan, 1922 (the species *buettikoferi*, *corbali*, *nigrofasciatus* [in part], *longipinnis* [now a synonym of *nigrofasciatus*; see Trewavas, 1973]); Thys van den Audenaerde, 1968a (the species *buettikoferi*, *corbali* and *ocellifer*, with which *nigrofasciatus* was synonymised—but see Trewavas, 1973 for a correction of this misidentification); Trewavas, 1973 (the species *buettikoferi*, *nigrofasciatus* and *ocellifer*).

Paratilapia (in part): Boulenger, 1915 (the species *corbali* only).

Tilapia (in part): Thys van den Audenaerde, 1968b (the species *buettikoferi* and *ocellifer* (with which was included *nigrofasciatus*)).

The *Pelmatochromis* generic concept has had a checkered history. Originally created by Steindachner for two species (one of which, *P. jentinki*, is now referred to *Tylochromis*; see Regan, 1922), the genus was expanded by Pellegrin (1904) to include 18 species. Boulenger (1915) continued this expansion by raising the number to 36. Regan's (1922) far more critical review of the 'generic' characters then recognised, reduced the number of species to 24. Thys' (1968a) review of Regan's *Pelmatochromis* concept actually increased the species number to 27. But, unlike previous revisors, he recognised the polyphyletic nature of the assemblage, breaking it down into a number of what he called 'natural groups' (Thys, 1968a:382). As an interim measure he designated those groups as subgenera.

The nominate subgenus in Thys' scheme contained but two species, *P. buettikoferi* and *P. corbali*, which, however, he thought were probably conspecific although he did not formally synonymise the two taxa.

The most recent revision (Trewavas, 1973) recognises three species (*P. buettikoferi*, *P. nigrofasciatus* and *P. ocellifer*, the latter being one of the species treated by Thys (1968a) as a *Pelmatochromis* of uncertain subgeneric affinity, but which he later [1968b] transferred, with the other two, to *Tilapia*). Trewavas (*op.cit.*) makes no reference to *P. corbali*, presumably accepting Thys' (1968a) view that it is a synonym of *P. buettikoferi*.

One reason for this conceptual instability, at least when seen in retrospect, would seem to be the persistent lack of any critical definition for the genus. That is to say, a definition based on derived characters uniquely shared by all the constituent species. In every definition to date, the characters used are either plesiomorphic ones or, if apparently derived ones (like the unicuspid jaw teeth and cycloid scales), are widely distributed amongst other taxa. Those other taxa, however, are each definable on the basis of their own and uniquely shared synapomorphies, suggesting that the apomorphies shared with *Pelmatochromis* are either homoplasies or features indicative of relationship at a very distant level. In other words, *Pelmatochromis* is, and always has been defined and categorised on the absence rather than the presence of defining features, a sort of monophyly by default. Its real monophyly has yet to be established.

Thys (1968a) defined the subgenus *Pelmatochromis* (*Pelmatochromis*) on the basis of its members possessing microbranchiospines (absent in members of all his other named *Pelmatochromis* subgenera, but present in one of his unnamed groups) and not having a *Tilapia*-spot, but instead a dark blotch (the so-called *Pelmatochromis*-spot) on the flank immediately below the soft dorsal fin.

The presence of microbranchiospines cannot be considered a derived feature within the Cichlidae (see Stiassny, 1981). The absence of a *Tilapia*-spot might, on the other hand, seem to be an apomorphy since its presence is apparently a plesiomorphy amongst African cichlids (Oliver, 1984; personal observations). Furthermore, it would seem that a *Pelmatochromis*-spot could be interpreted as a derived condition of the plesiomorphic *Tilapia*-spot. However, a *Tilapia*-spot is present in two of the three *Pelmatochromis* species (see Trewavas, 1973:12), and in one of these (*P. nigrofasciatus*) it sometimes occurs in combination with an incipient *Pelmatochromis*-spot (*op.cit.*: 7). On the basis of those data, the presence or absence of a *Tilapia*-spot and, or, the presence of a *Pelmatochromis*-spot would be of doubtful value for establishing the monophyly of what is now the genus *Pelmatochromis*.

Three other seemingly derived features of *Pelmatochromis* (cycloid scales, unicuspid jaw teeth, and the shape of the gill-rakers) must also be considered.

On the basis of outgroup comparisons amongst perciform fishes, tenoid rather than cycloid



Fig. 1 Anterior premaxillary teeth (frontal view) of *Pelmatochromis buettikoferi*. Magnification $\times 16$ (BMNH 1911.5.31:47).

scales should be considered plesiomorphic. The situation within the Cichlidae is, in my view, less readily interpreted (see discussions in Greenwood, 1979, and Oliver, 1984). If, as Oliver (1984) argues, cycloid scales are to be treated as apomorphic (i.e. derived) features in the Cichlidae, then I would agree with his further suggestion that they '... arose two or more times in the family'. The value of cycloid scales for establishing the monophyly of *Pelmatochromis* can, however, be discounted since the scales in all pelmatochromine taxa are predominantly of that type.

Large specimens of all three *Pelmatochromis* species have, in the outer row of both jaws, teeth which are relatively slender unicuspid, their crowns somewhat attenuated and slightly compressed (Fig. 1). Such unicuspid teeth can, in my opinion, be considered an apomorphic feature within the cichlids, even though unicuspid occur commonly amongst percoid outgroups. My argument for considering unicuspid teeth in cichlids as a derived feature is as follows:

- i. Unicuspid teeth in such basal percoids as the Serranidae and Centropomidae are small, very numerous and form a relatively dense felt on the alveolar surface of the dentigerous jaw bones, with no clear differentiation between outer and inner tooth rows. In cichlids with unicuspid teeth, those in the outer row are clearly larger than the inner row teeth, are usually separated from the latter by a distinct gap, are well separated from one another and, relative to the basal percoid type, are larger.
- ii. Whenever it has been possible to study the post-larval ontogeny of jaw teeth in cichlids, a definitive unicuspid dentition in the outer tooth rows is preceded by one of essentially bicuspid or weakly bicuspid teeth in which the minor cusp forms a sort of shoulder to the major cusp (Greenwood, 1974; 1982). Such early bicuspid teeth may be interpreted as an interim dentition since, in the few examples studied, the earliest recognisable jaw teeth present in buccal larvae are very fine, needle-like objects (see Greenwood, 1956:228 for haplochromines; Fishelson, 1966:596-7 and fig. 28 for *Tilapia tholloni* where the teeth are described as tricuspidate but the photograph indicates otherwise; and Balon, 1977:165 for *Labeotropheus* species).

The occurrence of some bicuspid teeth in *P. nigrofasciatus* was noted by Thys (1968a:370; fig. 16), but at that time this species was misidentified as *P. ocellifer* (see Trewavas, 1973) and was thus not included in his subgenus *Pelmatochromis* (*Pelmatochromis*). These bicuspid teeth are discussed in detail by Trewavas (1973:6; fig. 4) who showed that distinctly bicuspid (i.e. 'notched') teeth in *P. nigrofasciatus* are found only in small fishes, and are less numerous than the slender conical ones

with which they occur. The sole specimen with notched teeth available to Trewavas is 22 mm SL; in the next larger specimen she examined (38 mm SL) notched teeth are absent and are replaced either by unicuspid or by very weakly bicuspid teeth in which the minor cusp is reduced to no more than a shoulder continuing the base of the major cusp towards the margin of the tooth (*op.cit.*, fig. 4). Such shouldered teeth, unlike the unicuspid teeth which replace them, have flattened and not conical crowns.

I have re-examined the small *P. nigrofasciatus* studied by Trewavas and can confirm her observations. Furthermore, I find that in two larger individuals (100 and 109 mm SL, MRAC 52454–5 identified by Trewavas) some outer teeth situated posterolaterally in the dentary have faint indications of a shoulder and, like definitely shouldered teeth, have an obliquely cuspidate and compressed, not conical, major cusp. Similar shadow-shouldered teeth occur in a 65 mm SL specimen (from MRAC lot number 118090–99), which also has some more obviously bicuspid (i.e. notched) teeth amongst the unicuspid teeth. In both these specimens the non-unicuspid teeth are not restricted to any particular region of the jaw.

Shadow-shouldered teeth, identical with those in *P. nigrofasciatus*, occur amongst the slender, conical-crowned unicuspid teeth in the outer tooth rows of both jaws in the holotype of *P. ocellifer*, a specimen of ca. 65 mm SL. Many teeth are missing from this now poorly preserved specimen but it seems likely that the shadow-shouldered forms were confined to the anterior and anterolateral regions of the jaws.

Thus, *pace* Trewavas (1973:14) it seems that barely recurved, weakly shouldered teeth, quite unlike the definitive conical-cuspid and moderately recurved unicuspid teeth, occur in small specimens of at least two *Pelmatochromis* species, and that some may persist in larger individuals. Trewavas, on the contrary, believed that in *P. buettikoferi* and *P. ocellifer* the ‘... outer teeth are curved and conical at all stages from a standard length of 28 mm’.

Teeth in the inner rows, at least in *P. nigrofasciatus* (Trewavas, 1973:12) also undergo an ontogenetic change in form, being unicuspid in fishes of 68 mm SL and above, but shouldered in smaller individuals. However, the inner teeth in the smallest *P. ocellifer* and *P. buettikoferi* examined are all small and slender unicuspid teeth.

The ontogenetic changes leading to a unicuspid adult dentition in the jaws of two *Pelmatochromis* species would seem to reinforce the assumption that the definitive dentition in this taxon represents a derived condition. A unicuspid definitive dentition, of course, occurs in many cichlid genera (including other pelmatochromines), taxa which, in most cases, can be defined on the basis of their own autapomorphic features, or which have other apomorphic characters not present in *Pelmatochromis*. Thus, in itself the unicuspid dentition of *Pelmatochromis* could as well be a synapomorphic character indicative of that taxon's membership in some larger phyletic assemblage, rather than an autapomorphy for the genus alone. Without the support of other congruent autapomorphies it does not establish the monophyly of the genus.

The third apparently derived feature shown by *Pelmatochromis* concerns the morphology of the gill-rakers (Fig. 11). Although there is a very wide range of gill-raker form, size and arrangement in African and in Neotropical cichlids, the rakers in the outer row on the first gill-arch in all three *Pelmatochromis* species are of a type rarely encountered in the family. They are also quite unlike those found amongst other members of the Labroidei (the suborder to which the cichlids belong) or in the majority of percoid fishes. On those grounds I would consider that the rakers in *Pelmatochromis* are indeed apomorphic. But again, there is the problem of whether or not the character is an autapomorphic one, and thus indicative of the taxon's monophyly (see below).

The outer ceratobranchial gill-rakers in *Pelmatochromis* are moderately long, pachydermatous structures, so arranged on the greater part of the arch as to be directed obliquely forward across its surface and not, as is the usual condition, pointed aborally away from the arch. In outline each raker is approximately crescentic (the concave face uppermost), deep over most of its length but with the distal part drawn out rather abruptly into a fine, bluntly pointed, horn-like tip. Proximally at least, the membrane covering the bony skeleton of the raker is continued medially where it meets a prominent ridge of tissue running a little medially to the midline of the arch. Between each of the rakers of the inner and outer rows this ridge is drawn-up into a prominent but low papilla. Over the concave upper surface of each raker (but most noticeably in those on the middle section of each

arch) its covering tissue is thrown into numerous, contiguous, low tubercles, so that the raker comes to resemble the chela of a crab's claw (albeit a rather compressed one).

The inner rakers of this arch are shorter than their outer counterparts, and are subconical in shape; as in the outer rakers, the aboral surface is tuberculate. Inner and outer row rakers are virtually continuous, the gap between them being filled by the low papilla noted above.

There is apparently some interspecific variation in the morphology of the outer rakers on the first arch, both in the extent to which the distal 'horn' is produced (and thus is more or less obvious and horn-like) and in the degree to which the aboral face is tuberculated. Since, however, these features are formed in soft tissue it is possible that both could be influenced by fixation and preservation, by the time for which the specimen has been preserved, and by prefixation *post-mortem* changes.

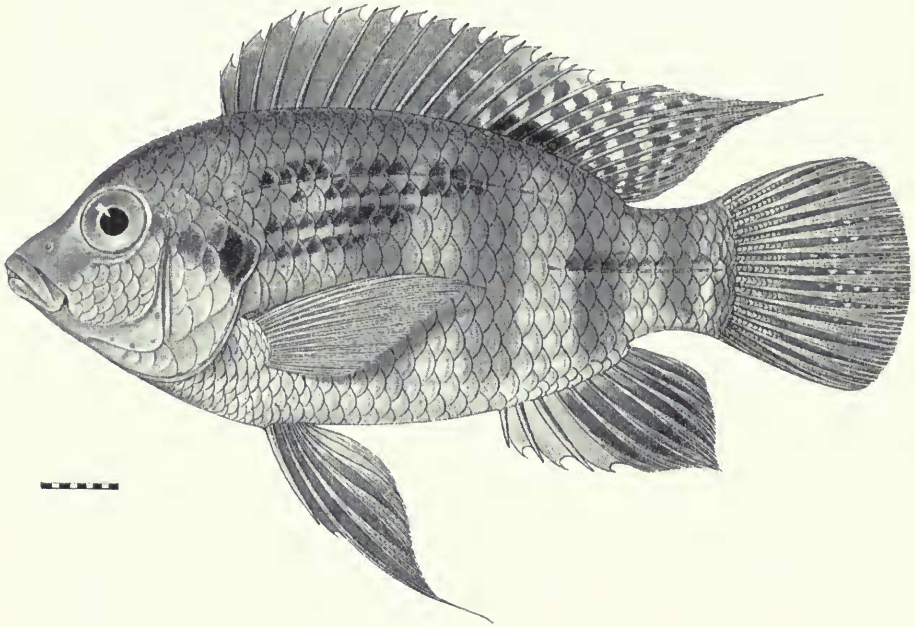


Fig. 2 *Pelmatochromis ocellifer*; from the original drawing by J. Green. Scale bar in mms.

Both rows of gill-rakers on the epibranchial part of the first arch are simple, slender and relatively long, and are implanted at right angles to the arch's surface.

Although the ceratobranchial gill-rakers in *Pelmatochromis* can be ranked as an apomorphic feature, it is difficult to decide whether they should be considered an autapomorphy for the genus rather than a synapomorphy shared with most other pelmatochromine taxa except *Pterochromis* (for which see p. 155).

Allowing for possible influences of preservation and other chance factors, gill-raker morphology in these other taxa seems merely to be an intensification of certain details (tuberculation, thicker epithelial cover, and greater attenuation of the horn-like tip) found in *Pelmatochromis*. On the present evidence I would withhold a final judgement on that point, but would note here that the evidence suggests synapomorphy rather than autapomorphy (see p. 191).

Since none of the three presumed apomorphic features of *Pelmatochromis* can be established unequivocally as an autapomorphy, the monophyly of the genus still cannot be established. Its status as a discrete taxon is based only on its possessing a suite of characters, both apo- and plesiomorphic which, taken in combination, differentiate it from other superficially similar taxa.

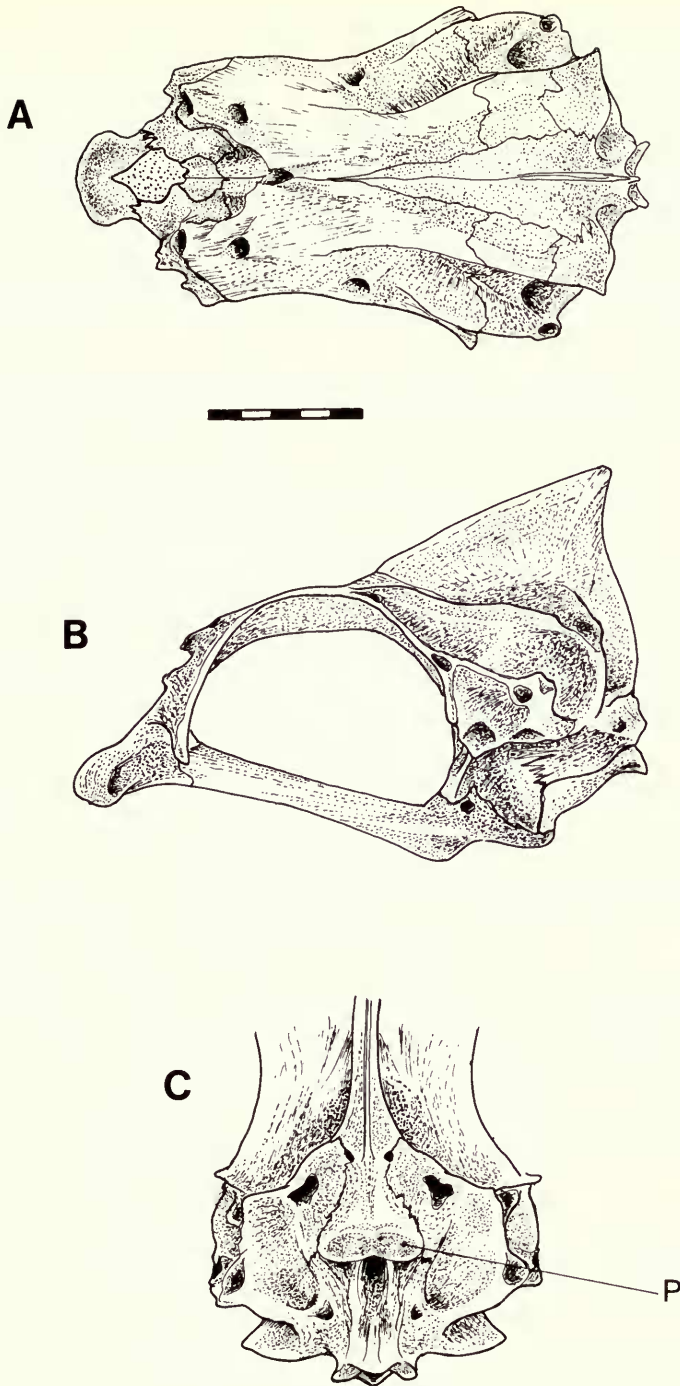


Fig. 3 *Pelmatochromis buettikoferi*. Neurocranium in: A. Dorsal; B. Left lateral view. C. Neurocranial apophysis for the upper pharyngeal bones. P = parasphenoid. Scale bar in mms (BMNH 1911.5.3:48).

Interestingly, Trewavas (1973:19) commented that ‘... the adult dentition of *P. nigrofasciatus* is itself so distinct as to suggest that *Pelmatochromis* is diphyletic’, but did not develop her argument further nor, in that particular context, did she indicate the nature of the distinction. Presumably she is referring to the size discrepancy between inner and outer row teeth in this species as compared with the condition in other *Pelmatochromis* species, and to the slight posterior broadening of the inner tooth rows of the dentary. In the absence of any other seemingly autapomorphic morphological features in *P. nigrofasciatus* (its reproductive isolation is assumed), or derived features shared uniquely by the two other species, the possibility of the genus being non-monophyletic can no more be established than can its monophyly.

The interrelationships of *Pelmatochromis* are discussed on p. 192 below.

DIAGNOSIS. Several of the features noted here are discussed in more detail on pp. 149–153. *Pelmatochromis* is distinguished from other genera of African cichlids by the following characters taken in combination:

Body moderately deep (Fig. 2), not fusiform.

Neurocranial apophysis for the upper pharyngeal bones formed from the parasphenoid alone

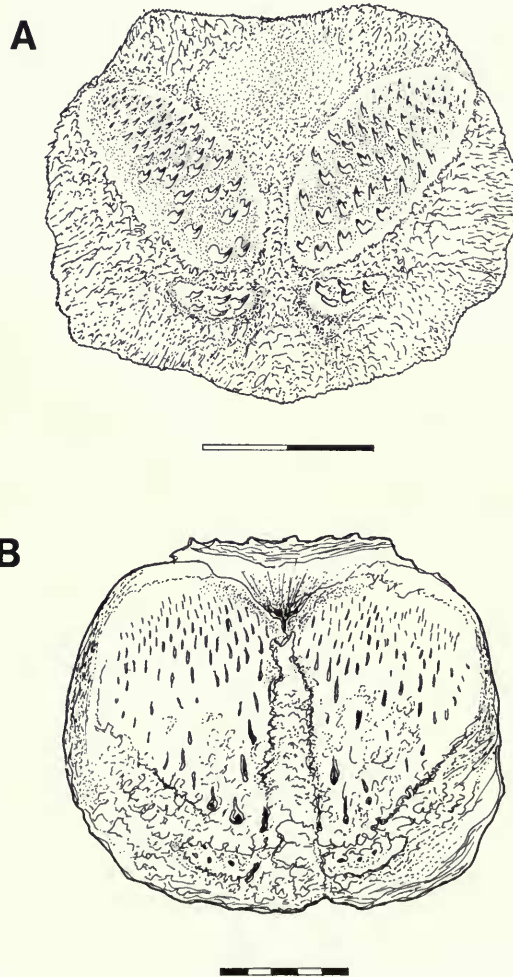


Fig. 4 Occlusal view of the upper pharyngeal bones, *in situ*, of: A. *Parananochromis longirostris* (BMNH 1903.7.28:77–83), and B. *Tilapia zillii* (BMNH 1973.3.27:7–8). Scale bar in mms.

(i.e. of the *Tilapia*-type; Fig. 3C); supraoccipital crest prominent (Fig. 3B); supraethmoid not contacting the vomer (at least in *P. buettikoferi*).

Palatine with a two-point neurocranial contact, anteriorly through an articulation in the region of the ethmovomerine suture, and posteriorly with a facet on the ventral face of the lateral ethmoid (see Greenwood, 1985a); a calyx present between the metapterygoid and the hyomandibula (see Greenwood, 1985a; 1986).

Prepharyngeal pad in the bucco-pharyngeal roof prominent but not developed into a visor-like hanging pad clearly demarcated from the surrounding tissue. Posterior facing margins of the major upper pharyngeal bones (the fused pharyngobranchials 3 and 4) so aligned as to form a broad and shallow V whose apex is directed anteriorly (see Fig. 4A). No 'kukri'-shaped teeth on the lower pharyngeal bone (see p. 197 and Fig. 30), the teeth of which all have the tip of the major cusp pointing forwards and lying a little anterior to, or in the same vertical as the tooth's posterior margin. Anterior blade of the lower pharyngeal bone short, its length contained 3–4 times in the overall length of the bone.

Infraorbital bones forming a complete lower and posterior margin to the orbit, the first infraorbital (lachrymal) longer than deep and with 4 openings to its laterosensory canal (Fig. 5A).

Outer row jaw dentition, at least in fishes > 25 mm SL, composed predominantly of slender and slightly recurved unicuspid teeth with attenuated conical crowns (Fig. 1); in smaller specimens some weakly cuspidate teeth with notched or shouldered crowns also occur (see p. 144); inner tooth rows are composed mainly of slender unicuspid teeth.

Ascending process of the premaxilla 30–35 percent of head length. Anguloarticular with roofed canal for the mandibulo-preopercular laterosensory canal. Lower jaw length less than half head length.

Scales cycloid, 25–30 pored scales in the lateral-line series; upper lateral-line clearly separated from the dorsal fin base over the line's entire length, and by at least $2\frac{1}{2}$ or 3 scales at its highest point (*ca* the 8th scale in the series), and by $1\frac{1}{2}$ or 2 scales over the last pored scale; 16 scales around the caudal peduncle. Cheek with 3 scale rows. Chest scales not noticeably smaller than those situated anteriorly on the ventral and ventrolateral aspects of the flanks and belly.

Gill-rakers in the outer row on the ceratobranchial of the first gill-arch number 14–16, are transversely orientated across and close to the arch, are long, pachydermatous and crescentic, have the concave upper surface tuberculate, and the distal tip produced and horn-like. These rakers are continuous with a prominent projection developed from the membranous ridge extending down the middle of the gill-arch (see p. 145). Gill-rakers on the epibranchial of the first arch number 3–8, are simple, relatively slender and elongate, and are arranged in two rows.

Microbranchiospines present on the outer face of gill-arches 2–4.

Modal total number of vertebrae 25; there are 13–15 (mode 14) abdominal and 10–12 (mode 11) caudal vertebrae (all counts exclude the fused PU1 and U1 centra). Spondylophysal apophysis for the retractor pharyngeal muscles well-developed and situated on the 3rd centrum.

A single supraneural (predorsal) bone. Dorsal fin with 13–15 spines, anal fin with 3 spines.

Tilapia-spot present in at least the young of two species, 'replaced' ontogenetically in one of those species by a *Pelmatochromis*-spot which is also present in a third species that never develops a *Tilapia*-spot (see Trewavas, 1973 and p. 143 above).

All species are substrate guarders.

NOTES ON THE ANATOMY AND OTHER FEATURES. Anatomical and osteological studies have been made principally on the type species, *P. buettikoferi*, but certain osteological features were checked from radiographs and by superficial dissections of *P. ocellifer* and *P. nigrofasciatus*.

In most features the cranial and pharyngobranchial myology, osteology and arthrology of *P. buettikoferi* depart but slightly, if at all, from what seemingly can be taken as the modal and plesiomorphic condition for African cichlids. In an intrafamilial context there are few derived features (see Barel *et al.*, 1976; Cichocki, 1976; Anker, 1978; Stiassny, 1981a & 1982; Greenwood, 1983 & 1985a).

Osteology. The *neurocranium* (Fig. 3) has the plesiomorphic *Tilapia* type of apophysis for the upper pharyngeal bones (Greenwood, 1978) in which the entire articular surface is contributed by the

parasphenoid. The skull (Fig. 3) is relatively foreshortened and broad interorbitally, and the ethmovomerine region is somewhat decurved, sloping downwards at an angle of *ca.* 50° to the horizontal.

The ethmovomerine length (measured directly from the anterior tip of the vomer to the lateral tip of the lateral ethmoid) is short and is contained about $3\frac{1}{4}$ times in the neurocranial length (measured directly from the anterior tip of the vomer to the ventral rim of the basioccipital facet). At least in *P. buettikoferi* (the other species could not be examined) the supraethmoid does not contact the vomer, an unusual feature (see Trewavas, 1973; Greenwood, 1985a) but one of as yet indeterminable phylogenetic significance.

In *P. buettikoferi* (again the only species which could be checked) the lateral commissure of the *pars jugularis* is of the *Haplochromis*-type, and there is a stout precommissural bridge between the

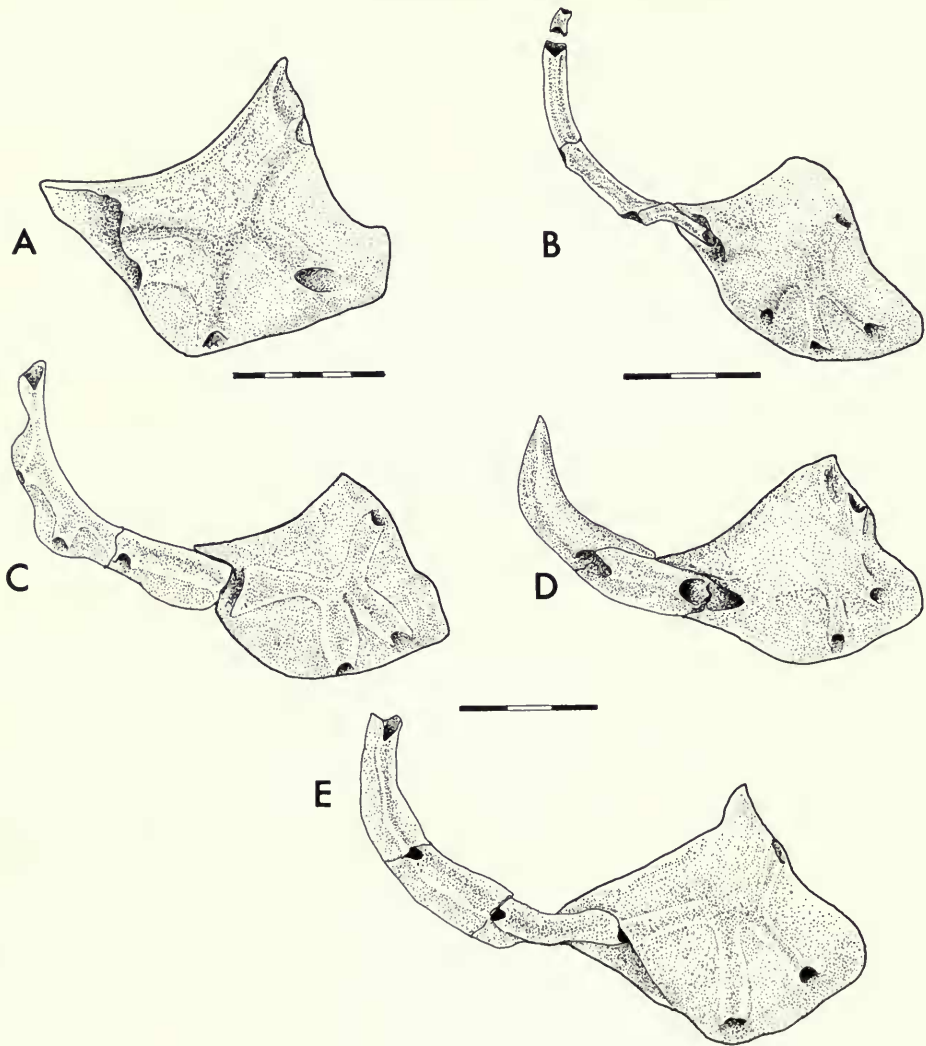


Fig. 5 Right infraorbital bones of: A. *Pelmatochromis buettikoferi* (lachrymal only); B. *Chromidotilapia guntheri* (lachrymal+4 others); C. *Parananochromis longirostris* (lachrymal+2 others); D. *Pelvicachromis pulcher* (lachrymal+2 others); E. *Thyisia ansorgii* (lachrymal+2 others). Scale bar in mms.

prootic and pterospheoid bones (see Greenwood, 1986). An *Haplochromis*-type lateral commissure is a plesiomorphic feature, but the significance of a precommissural bridge is still unknown (Greenwood, *op.cit.*).

The supraoccipital crest is well-developed and relatively long basally, its anterior point lying above about the mid-point of the orbit.

The *infraorbital bone series* (Fig. 5A) is complete, with almost half the second ossicle overlapping a posterior, plate-like flange developed below and behind the posterior lateral-line canal opening of the lachrymal. There are four lateral-line canal openings in the lachrymal, the presumed plesiomorphic condition in cichlids (Trewavas, 1983; Greenwood, 1985a).

Few characters associated with the *pharyngobranchial skeleton* in *P. buettikoferi* require comment. There is a very broad and elongate, near-rectangular cartilaginous expansion of the second epibranchial's anterior margin (see fig. 11 in Trewavas, 1973). This process is partly lodged within the body of the prepharyngeal pad. From my own observations on a number of African cichlids there is apparently little or no correlation between the extent to which the cartilage is developed and the degree to which the pad is developed, unless it is of the hanging pad type. For instance, in both *Orthochromis machadoi* and *Hemichromis bimaculatus* the prepharyngeal pad is very well-developed and approaches the visor-like hanging pad found in several pelmatochromine taxa (but not *Pelmatochromis*). Yet, in *O. machadoi* and *H. bimaculatus* the cartilage is very poorly developed (Greenwood, 1984a & 1985a). It seems, however, that in species with a fully-developed hanging pad the cartilage is always extensive (personal observations on various pelmatochromine species, and in those members of the *Ophthalmotilapia* assemblage from Lake Tanganyika which have a hanging pad; see Greenwood, 1983). Unfortunately, this cartilage is invariably shrivelled in dry skeletons, and to date few alcian-blue counterstained alizarin preparations are available for study. Thus the validity and significance of my few observations cannot be tested. It should be noted that in the *Tilapia busumana* dissected for this purpose, the cartilage is as extensive as that in the *Pelmatochromis nigrofasciatus* illustrated in fig. 11 of Trewavas (1973), and does not resemble the smaller and very differently shaped cartilage that author shows for *T. busumana*. It is difficult to tell, however, whether these differences are attributable to intraspecific variability or to the techniques used for preparing the specimens.

The quadrangular area of epibranchial 4 in *P. buettikoferi* is deep and near-rectangular, and the shank spine is ridge-like; the bone thus closely resembles that of *Chromidotilapia kingsleyae* illustrated by Greenwood (1985a; fig. 15B).

The *lower pharyngeal bone* in all species (Fig. 6A; and figs 5A–D in Trewavas, 1973) has a short anterior blade (*ca.* $3\frac{1}{2}$ –4 times in the overall length of the bone, measured as the vertical between the tip of the blade and the tips of the articular horns). Its posterior margin has a deep median indentation so that the outline of the bone is distinctly arrow-head shaped. There are some, slight, interspecific differences in the lower pharyngeal dentition (see Trewavas, 1973), but no major modifications are apparent in tooth shape or cusp form, which are essentially of the generalised African cichlid type (see p. 197 for a description and discussion of the 'kukri'-shaped teeth in tilapiines). The upper pharyngeal teeth are likewise of a generalised type. The *upper pharyngeal bones* (pharyngobranchials 2 and 3+4, the former lying anterior and closely apposed to the latter) are so arranged that the posterior facing medial margins of the fused third and fourth pharyngobranchials of each side form a broad and shallow V. The apex of the V, the second pharyngobranchials, is directed anteriorly (Fig. 4A). In outline the fused third and fourth pharyngobranchials are narrowly sub-ovoid. A broadly V-shaped arrangement of the upper pharyngeal bones is the plesiomorphic condition for both the African and Neotropical cichlids (see discussion on p. 198).

Little comment is required on the *caudal fin and axial skeleton*, except to note that the single supraneural bone is well-developed, that there is (at least in *P. buettikoferi*) a stout and prominent spondylophysal apophysis on the third centrum, and that the number of vertebrae is low, both in total and in separate counts of abdominal and caudal elements. Again, this is the plesiomorphic condition. In all three species there are 13–15 (mode 14) abdominal vertebrae and 10–12 (mode 11) caudal elements, giving total counts of 24–26 (mode 25); the fused PUI and UI centra are not included so that the total is lower than that given by Trewavas (1973).

No outstanding features were noted in the skeleton of the *jaws*, or in the *suspensorium* and *palatoquadrate arch*.

A distinct calyx formed from the metapterygoid and hyomandibula, and open medially, is present (see Greenwood, 1985*a*), and the mandibulo-preopercular laterosensory canal passes through a roofed canal in the anguloarticular bone (see Greenwood, 1985*a* & *b*). There are five

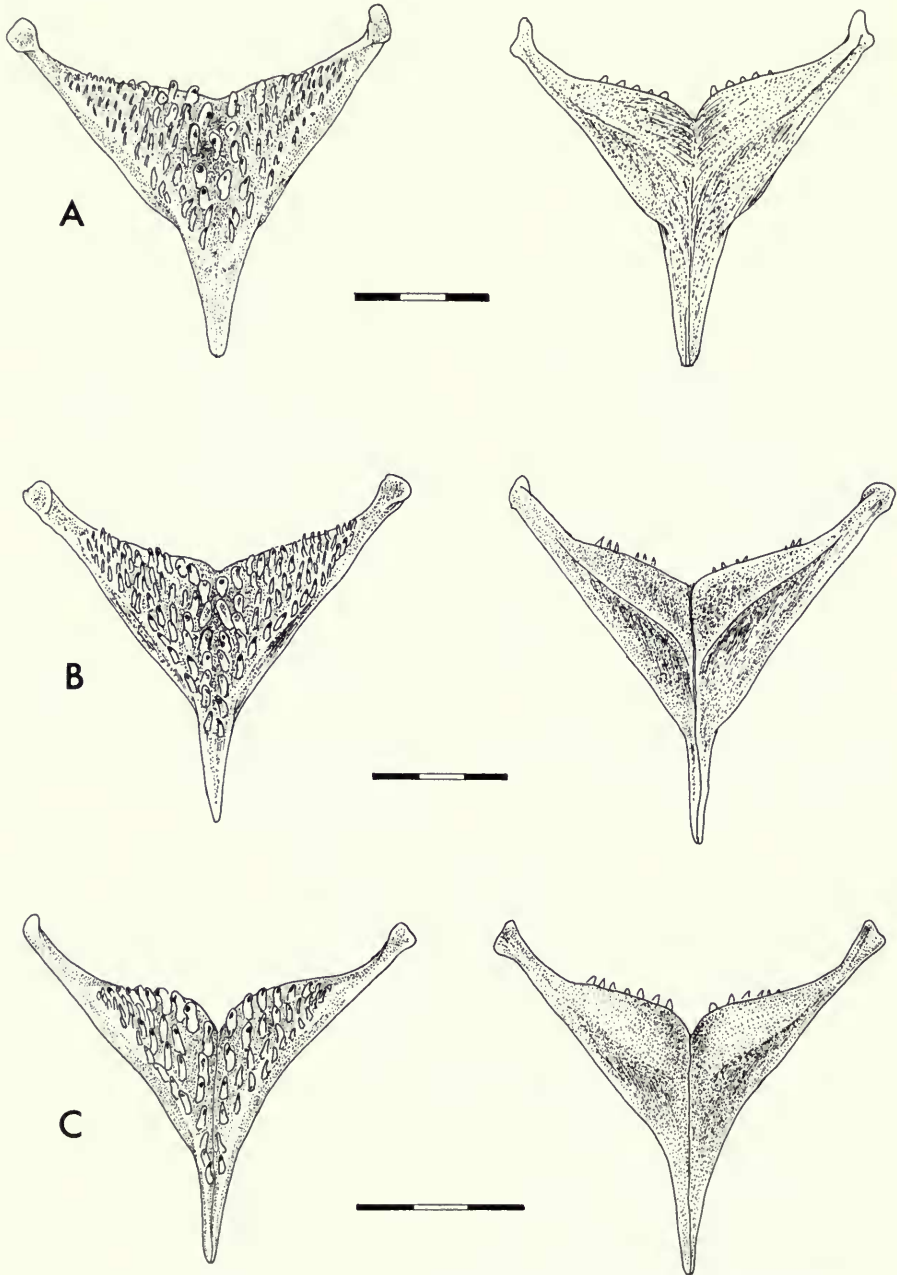


Fig. 6 Lower pharyngeal bone, in occlusal (left) and ventral (right) views, of: A. *Pelmatochromis buettikoferi*; B. *Thysia ansorgii*; C. *Chromidotilapia finleyi*. Scale bar in mms.

laterosensory openings in the dentary and seven in the preoperculum; that is, the usual number amongst African cichlids and in the majority of Neotropical taxa as well. Both these conditions are plesiomorphic for cichlids, but the calyx is a widespread apomorphy in the family.

Squamation. The scales in all *Pelmatochromis* species are predominantly cycloid ones, with a few weakly granular scales sometimes occurring as well. Scales on the chest are not noticeably smaller than those on the belly and ventrolateral aspects of the flanks, and what size change there is takes place gradually. The cheek is completely scaled, being covered by three rows at its deepest point. The upper lateral-line is, at its highest point, separated by at least $2\frac{1}{2}$ scale-rows from the dorsal fin base, and there are at least $2\frac{1}{2}$ scale-rows above the last pored scale in the series. There are 16 scales around the caudal peduncle, the commonest and probably plesiomorphic condition in African cichlids.

Fins. No sexual dimorphism is apparent in the shape of the caudal fin, which has a gently rounded margin. Neither is there a marked dimorphism in pelvic fin shape. Here the first unbranched ray is clearly the longest in both sexes although, relatively, that ray may be longer in males than females; however, the small sample sizes available for all species, and the difficulty of sexing many of the specimens, require that observation to be checked.

Other external features and the *dentition* are discussed on pp. 143–145.

Myology and arthrology of the jaws and palatoquadrate arch. No really outstanding features were noted in either system of *P. buettikoferi*; both closely approximate to the generalised condition amongst African cichlids (see Anker, 1978; Stiassny, 1981*a* & *b*, & 1982; Greenwood, 1985*a*).

Tendon A1 β of the *adductor mandibulae* I muscle is very broad, and fuses completely with the tendon of adductor muscle Aw (i.e. like the condition in *Hemichromis* but unlike that of the other taxa examined; see Stiassny, 1981*a* & *b*; Greenwood, 1985*a* and unpublished observations). As in *Hemichromis* a discrete division of A1 β tendon inserts on the nipple process of the anguloarticular.

Muscle A3 of the *adductor mandibulae* complex is poorly developed, its anterior half being entirely tendinous. The *adductor arcus palatini* muscle has an extensive insertion on the palatine bone (see Greenwood, 1985*a*; 169).

The *dorsal gill-arch muscles* of *P. buettikoferi*, like the musculature of the jaws and palatoquadrate arch, are essentially similar to those of other generalised cichlids. They closely resemble *Hemichromis* (Greenwood, 1985*a*) in their general lay-out, although the relative size of certain muscles is different. The major association of the *levator externus* 4 with the horn of the lower pharyngeal bone is exactly as in *Hemichromis*. Also as in *Hemichromis*, only a small slip of the *levator posterior* muscle inserts on the horn, the major part of the muscle being inserted on the fourth epibranchial bone (see Greenwood, 1985*a*:159–162).

Muscles derived from the circumoesophageal series, and extending forward between the upper pharyngeal bones to insert on the 2nd and 3rd pharyngobranchials (Anker's [1978] 'sub-epithelium muscular tissue'), are well-developed. They originate as a single longitudinal band which bifurcates anteriorly at a point about two-thirds of the way along the length of the third pharyngobranchial.

Ventral gill-arch musculature. The *rectus ventralis* and the *obliquus ventralis* muscles have the same relationship with the semicircular ligament as do the muscles in *Hemichromis* and a number of other African and Neotropical species I have dissected (see Greenwood, 1985*a*; also unpublished observations, and p. 163 below).

The *transversus ventralis anterior* muscle is interrupted medially by the anterior blade of the lower pharyngeal bone, the common condition in African taxa (see Stiassny, 1982:442; fig. 13(a)).

Relationships. The virtual absence of unequivocally autapomorphic features amongst the characters studied makes it impossible to corroborate the assumed monophyly of *Pelmatochromis* (see p. 146 above). Likewise, the absence, except for one possible character, of synapomorphic features with a relatively restricted distribution amongst other cichlids, makes it impossible to hypothesise, with moderate certainty, a sister-group for the genus, or to suggest that its contained taxa be transferred to some other genus or genera. Certainly there is no evidence to support Thys' (1968*b*) idea of placing two species in the genus *Tilapia* (see also Trewavas, 1973), a problem discussed further on p. 195.

The single derived and possibly synapomorphic feature noted above is the morphology of the gill-rakers. It would certainly argue against a relationship with *Tilapia*, but does suggest

Pelmatochromis could be the plesiomorphic sister taxon to all the other pelmatochromines except *Pterochromis* (see p. 191).

Included species. *Pelmatochromis buettikoferi* Steindachner, 1894; *P. ocellifer* Boulenger, 1899; and *P. nigrofasciatus* (Pellegrin), 1900. For synonymies of these species see Trewavas (1973); in that work no mention is made of *P. corbali* (Blgr), 1913, which Thys (1968*a*) thought to be '... very nearly related and probably identical' with *P. buettikoferi*.

***PTEROCHROMIS* Trewavas, 1973**

TYPE SPECIES. *Pelmatochromis congicus* Boulenger (1897)

SYNONYMY. *Pelmatochromis* (in part): Pellegrin, 1904; Boulenger, 1915; Regan, 1922; Thys, 1968*a*. In all, only the species *congicus* is involved.

Tilapia (in part): Thys, 1968*b* (the species *congicus* only).

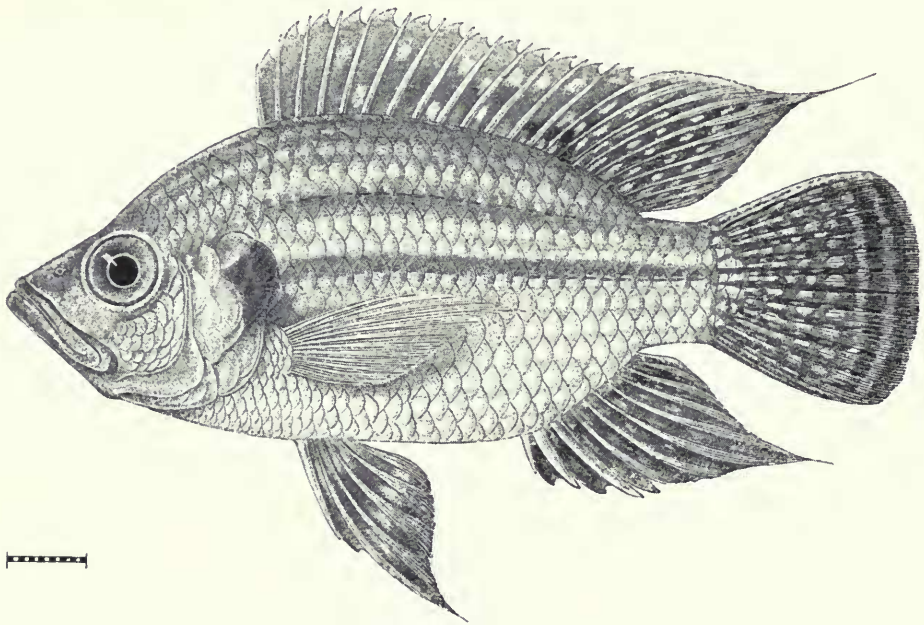


Fig. 7 *Pterochromis congicus*. From Boulenger, 1915; about natural size.

GENERIC STATUS AND RELATIONSHIPS. Thys (1968*a*) treated *congicus* as a species of *Pelmatochromis* but did not include it in any of his named subgeneric divisions. He did, however, group it with *P. ocellifer* (= *P. nigrofasciatus*, see Trewavas, 1973) and *P. ruweti* (now *Tilapia ruweti*), and indicated a possible relationship of the group with *Tilapia sparrmanii* (Thys, 1968*a*:381 and fig. 17). Later that year, Thys (1968*b*) formally included *P. ocellifer* and *P. congicus*, together with *P. buettikoferi* as a subgenus (*Pelmatochromis*) of *Tilapia*; *P. ruweti* was placed in the nominate subgenus *Tilapia*, together with *T. sparrmanii*.

Trewavas (1973) disputed Thys' reasoning (except that for including *P. ruweti* in *Tilapia*) and resurrected *Pelmatochromis* as a genus for the species *buettikoferi*, *ocellifer* and *nigrofasciatus* (see p. 143 above). Since, in her view, the species *congicus* could not be grouped with the other three species, and was not congeneric with any other taxon, she erected the genus *Pterochromis* for it alone.

I would concur both with Trewavas' view on the need to separate *congicus* from the other three

Pelmatochromis species, and with the generic status she accorded it. But, I would not support her contention that *Pterochromis congicus* '... is a specialised form' derived from *Pelmatochromis nigrofasciatus*, a relationship originally proposed by Thys (1968a; but see Trewavas [1973:10] regarding Thys' confusing *P. nigrofasciatus* with *P. ocellifer*, the latter name being used when he suggested the relationship of *P. congicus*).

Discounting the near impossibility of identifying an actual ancestral species, *Pterochromis congicus* and *Pelmatochromis nigrofasciatus* (or for that matter any *Pelmatochromis* species) have no shared derived features which might indicate their shared common ancestry. The resemblances rest almost entirely on symplesiomorphic characters, as for example the low vertebral counts, the *Tilapia*-type neurocranial apophysis, the presence of a *Tilapia*-spot in young fishes, a sessile pre-pharyngeal pad, microbranchiospines being present, the position of the upper lateral-line relative to the dorsal fin base, the size of the scales (27–28 in a lateral series), the elongate first pelvic fin ray, and the sexually monomorphic caudal fin shape.

Apart from its autapomorphic features (see below), *Pterochromis* has two characters, cycloid scales and unicuspid outer row jaw teeth, which could be considered apomorphic, and which are also shared with *Pelmatochromis* (and other taxa outside the pelmatochromine assemblage as well). The polarity and significance of these characters are discussed on pp. 143–145. If it be accepted that both are apomorphies, then their widespread occurrence amongst African cichlids reduces their value as indicators of recent shared common ancestry, especially when no other and congruent synapomorphies are shared by the taxa under review. In the case of *Pterochromis* and *Pelmatochromis* there are apparently no such congruencies. The presence of unicuspid teeth and cycloid scales in *Pterochromis* could as well indicate relationship with *Hemichromis* as with *Pelmatochromis* if comparisons are limited to west African taxa, and could even indicate affinity with taxa in other parts of the continent. But in every instance there are no features to support that relationship, and several characters to refute it.

Some of the characters used by Trewavas (1973) to distinguish *Pterochromis* from *Pelmatochromis*, namely the long, slender gill-rakers, the long ascending processes of the premaxillae and the elongate lower jaw, would at first glance seem to be apomorphic features.

Chief amongst these are the gill-rakers. Long, slender, untoothed, and numerous gill-rakers in the outer row of the first ceratobranchial are of uncommon occurrence in the Cichlidae, both African and Neotropical. They are not found in those African taxa which, on the basis of their few derived features, are taken to represent a plesiomorphic morphotype; for example *Heterotilapia multispinus* (see Oliver, 1984), *Pelmatochromis* (see p. 153) and *Astatotilapia* (see Greenwood, 1979 & 1980). However, long and slender rakers are common in other percoid groups, including members of the Labroidei, the suborder in which cichlids are currently classified. In most of these species, however, the rakers are tooth-bearing, as they are in the neotropical cichlid *Cichla* (whose derived or primitive status is disputed; see Stiassny, 1982).

Thus, the gill-rakers in *Pterochromis* could be interpreted as a plesiomorphic feature, but one showing partial derivation since the teeth are lost. Alternatively, the gill-rakers could be neomorphs which, in most respects, mimic the primitive condition. For the moment I see no means of resolving that ambiguity other than by applying the principle of parsimony, and concluding that the feature is indeed a plesiomorphic one.

Likewise I find difficulty in assessing the polarity of the probably correlated features of long ascending processes on the premaxillae, and a long lower jaw. Both are characters which occur in African cichlids and in out-group percoids as well. The upwardly inclined mouth (a feature not necessarily correlated with the elongate lower jaw and long premaxillary process) would, on the basis of both out- and intragroup comparisons, seem to be an apomorphy, albeit one which has evolved on several occasions.

One group of characters, the nature of the lower jaw dentition and dental arcade, not used by Trewavas (1973) in her generic diagnosis but noted in the generic description, is clearly an autapomorphy for *Pterochromis*. In that jaw the outer teeth situated anteriorly and immediately anterolaterally are several times larger and coarser than other teeth in the row, and are somewhat procumbently implanted. Their distinction is enhanced by the shape of the dental arcade which is noticeably angled medially for a short section of its length immediately behind the enlarged anterior

teeth. Indeed, the small unicuspid teeth in that sector of the outer row seem to be continuous with the outermost row of inner teeth. This impression is enhanced both by the rather irregular serial arrangement of the inner teeth, and by those teeth being restricted to a transverse arc across the anterior and anterolateral part of the dentary.

Once again, as is so often the case with cichlid fishes, the characters which serve to distinguish a taxon give no indications of its phyletic relationships.

DIAGNOSIS. As for *Pelmatochromis* (p. 148) except that:

- i. The unicuspid outer-row jaw teeth are relatively coarser in the upper jaw, and have only slightly recurved tips. In the dentary, the outer teeth situated anteriorly and immediately anterolaterally are much larger and coarser than the succeeding teeth in the row, and are implanted so as to slope forwards; the anterior teeth are somewhat isolated from the others since anterolaterally the row has a noticeable, and rather abrupt, mediad inclination, thus appearing to become continuous with the outermost row of the inner tooth-series (see fig. 8 in Trewavas, 1973).
- ii. The mouth (Fig. 7) is inclined upwards at a noticeable angle (*ca.* 45° to the horizontal). The ascending processes of the premaxillae are long (42–44 percent of head length), their tips reaching a point just before the anterior tip of the supraoccipital and lie above about the centre of the orbit; lower jaw also long (50–55 percent of head length).
- iii. Upper lateral-line, at its highest point, separated from the dorsal fin base by $3\frac{1}{2}$ or 4 scales; posteriorly there is one large and one very small scale between the last two pored scales and the dorsal fin base.
- iv. Gill-rakers in the outer row of the first ceratobranchial are numerous (17–19), long, smooth and fine (i.e. flattened, bristle-like structures), and are implanted at approximately right angles to the surface of the arch. Rakers on the first epibranchial are slender, but are shorter proximally; arranged in two rows, with 9–11 in the outer row.
- v. 13 abdominal and 12 caudal vertebrae (total count 25).
- vi. Dorsal fin with 13–14 spines.
- vii. *Tilapia*-spot on the dorsal fin but no indications of a *Pelmatochromis*-spot (see p. 143).
- viii. Breeding habits unknown.

NOTES ON THE ANATOMY AND OTHER FEATURES. Because so little study material is available, few observations could be made on the soft anatomy or the osteology of *Pterochromis congicus* (the sole representative), other than those which can be gleaned from superficial dissections and from radiographs.

Judging from the latter, the *neurocranium* has an outline very similar to that of *Pelmatochromis buettikoferi* (see p. 149, and Fig. 3). The ethmovomerine region is short and moderately decurved, and the supraoccipital crest is high, with its anterior part extending to a point over about the middle of the orbit. The apophysis for the upper pharyngeal bones, examined by dissection, is of the *Tilapia*-type (Greenwood, 1978).

The *infraorbital bone series* is complete, the lachrymal a long and relatively shallow bone with four openings to its laterosensory canal; the second infraorbital barely overlaps the posterior flange of the lachrymal.

No details of the *palatoquadrate arch* and the *suspensorium* could be seen from the radiographs, but a limited dissection showed a double palato-ethmoid articulation of the common cichlid kind (see Greenwood, 1985a:133–134 and 137–140). There are seven laterosensory canal openings on the *preoperculum*.

The *jaws*, apart from the long premaxillary ascending processes, and the peculiar dental arrangement in the dentary (see p. 155), provide no obvious points of comment which could be detected from a radiograph or which are visible externally. The passage of the laterosensory canal through the anguloarticular is roofed.

There are 13 abdominal and 12 caudal *vertebrae* (excluding the fused PU1 and U1 centra) in the two specimens radiographed; in one of these a large, well-developed spondylophysal apophysis is visible on the third centrum. As seen radiographically, the *caudal skeleton* has no distinctive features.

Little is known about the *branchial skeleton*, including the *pharyngeal jaws*. The lower pharyngeal bone is figured by Trewavas (1973: fig. 7). The upper elements have the same shape and spatial relationships as were described for *Pelmatochromis* (p. 151), and must be considered of the generalised and plesiomorphic cichlid type.

Squamation. Body scales in *Pelmatochromis congicus* are large and obvious; those on the chest have a gentle size-gradient with the scales on the ventrolateral aspects of the flanks, and although smaller are not noticeably so. Anteriorly, the upper lateral-line at its highest point (over the 8th pored scale) is separated from the dorsal fin base by $3\frac{1}{2}$ or 4 scales; posteriorly, the last two pored scales are separated from the fin base by one large and one very small scale. Save for a small naked area anteroventrally, the cheek is covered by three rows of scales.

Fins. There is apparently no sexual dimorphism in the shape of the caudal fin margin, which is very gently rounded. The first pelvic fin ray is clearly the longest.

With so few specimens known, it is impossible to be certain about the absence of sexual dimorphism in caudal and pelvic fin shapes, or of the significance to be attached, in that context, to the filament-like elongation of certain posterior rays in the dorsal and anal fins.

Relationships. There are no features which indicate that *Pterochromis* is closely related to any other pelmatochromine taxa, or on current evidence, to any other African lineage. Phylogenetically speaking it must be considered *incertae sedis*.

Included species: the type and only species *Pterochromis congicus* (Blgr) 1897.

II Pelmatochromines without microbranchiospines, and with a visor-like hanging pharyngeal pad

All taxa included in this pelmatochromine subdivision have a typical, visor-like and well-circumscribed projection of the pharyngeal tissues situated immediately anterior to the upper pharyngeal bones of each side (see p. 142; also Trewavas, 1974; Greenwood, 1983).

As conceived here, this subgroup also contains an assemblage which Thys (1968a:365, his species 17–21) maintained have '... a feebly developed or even no hanging pad on the roof of the pharynx'. I cannot agree with Thys on this point; specimens of all the named species he mentions (and one unnamed species, no. 21) have a distinctly visor-like pad. The pad is seemingly subject to the vagaries of preservation and curation (and possibly by the condition of the live fish too), and it can show intraspecific variability in its prominence. But, in its basic form and clear circumscription



Fig. 8 Dentary teeth (right) of *Pelvicachromis pulcher* to show characteristic shape of chromidotilapiine teeth; seen in near lateral aspect. Magnification $\times 29$ (BMNH 1901.11.28:13–20; a syntype).



Fig. 9 Right dentary of *Pelvicachromis humilis* to show the characteristic chromidotilapiine feature of the posteriorly directed teeth situated anterolaterally on that bone (BMNH 1972.3.16:8–10). Magnification $\times 14$.

from the surrounding pharyngeal tissue, it is always apparent in the specimens and species I have examined.

Microbranchiospines are absent in all members of group II pelmatochromines, a condition which is not necessarily correlated with the presence of a hanging pad since both structures are present in other cichlid genera (see Greenwood, 1983:267).

Both the presence of a hanging pad, and the absence of microbranchiospines can be ranked as synapomorphic features for this pelmatochromine group (see p. 191). Two other characters can be treated as congruent synapomorphies.

Throughout the size-range of specimens available to me, the outer row jaw teeth are characteristically shaped unicuspid. Unfortunately, those size ranges cover few small specimens of any species, and thus it has proved possible to trace the ontogenetic history of tooth form in only one species. No published information on that point is available either. In the exceptional species, *Chromidotilapia kingsleyae* (see p. 168), specimens 30–35 mm SL do have some teeth in which a very weak shoulder (see p. 145) is present, suggesting that at least weakly bicuspid teeth may precede the definitive and characteristic unicuspid of larger individuals.

The characteristic group feature of the definitive outer row jaw teeth concerns the shape of the crown. Whereas in *Pelmatochromis* and *Pterochromis* the crown is an attenuated cone (see Fig. 1), in this group it can be described as a unilaterally compressed cone, the compression being manifest on the labial aspect of the crown (Fig. 8). That is to say, in cross-section its labial face, relative to the lingual one, is flattened, although its surface is still clearly curved. As a consequence of this differential flattening, the anterior and posterior margins of the crown, especially near its tip, are relatively acute and ridge-like, not rounded as they would be in a uniformly conical one, and the crown comes to resemble the tip of a surgical suture needle. As compared with the crown of the teeth in *Pelmatochromis*, and especially that in *Pterochromis*, this part of the tooth in all group II pelmatochromines is more strongly recurved.

The second derived feature concerns the orientation, on both sides of the dentary, of the first few (1–4) teeth occupying an anterolateral position in the outer tooth row of that bone. In these teeth the curvature of the crown is directed posteriorly and not buccally as it is in all other teeth of the row (figs 9 & 10). Occasionally, in one species, the atypically orientated teeth occur unilaterally,

and there are indications in *Thysia* that such teeth appear late in the ontogenetic succession of tooth forms since posteriorly directed teeth are found only in specimens more than 95 mm SL.

A third derived feature, the form of the gill-rakers on the first ceratobranchial, is present in group II fishes, but its status as an autapomorphy is questionable; it could be a synapomorphy shared



Fig. 10 Right dentary (in part) of *Pelvicachromis pulcher* to show posteriorly directed anterolateral teeth and the general morphology of chromidotilapiine teeth (same specimen as Fig. 8). Magnification $\times 14$.

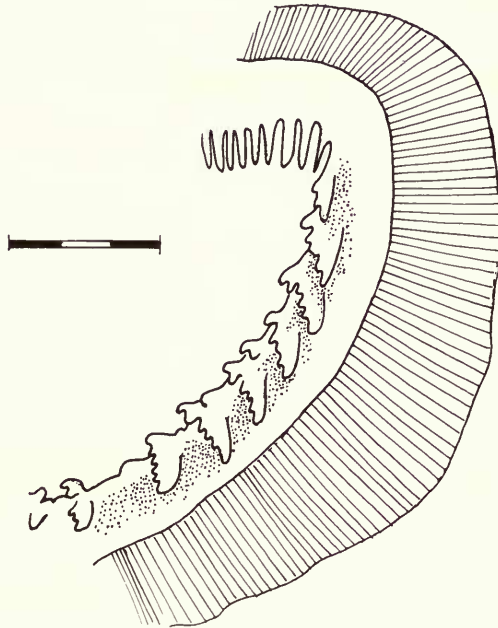


Fig. 11 Partially schematic drawing to show the general morphology of the gill-rakers on the first arch of a chromidotilapiine species. Modified after Trewavas (1974).

with *Pelmatochromis* (see p. 145). Basically, gill-raker morphology in both groups is similar (Fig. 11), the rakers being markedly pachydermatous, crescentic in shape, aligned transversely across and close to the arch, their tips produced into a horn-like projection, and the concave upper surface of the raker thrown into a number of low projections. Also common to both groups are the projections developed from the median membrane, and which are positioned between the rakers of the inner and outer rows. Again as in *Pelmatochromis*, the shape of the epibranchial rakers, as compared with the lower elements, is distinctly different, being dagger- or spear-shaped and inserted almost perpendicularly to the arch. However, in group II pelmatochromines the epibranchial rakers are reduced to a single row over much of that bone. Presumably the presence of a hanging pad contiguous with the proximal part of the arch inhibits the development of rakers in that region because a short inner row is present distally on the epibranchial.

In general, the outer row ceratobranchial rakers of group II species are thicker (i.e. more pachydermatous) than in *Pelmatochromis*, the upper surface is usually more tuberculate, and the distal tip appears more protracted and horn-like.

One other but polythetic feature may be an autapomorphy for group II pelmatochromines, and is discussed on p. 191.

On the basis of all constituent taxa sharing the apomorphic features discussed above (but with great reservation about the autapomorphic status of the gill-rakers), I would treat the group II species as a monophyletic assemblage. The possible relationships of that assemblage to *Pelmatochromis*, and the interrelationships of its constituent genera are discussed later (p. 191).

With one exception (the species *ansorgii*, see below) all the taxa treated here as members of group II, were placed by Thys (1968a) in one or other of three named subgenera, viz. *Chromidotilapia*, *Pelvicachromis* or *Nanochromis*, taxa raised to generic level by Thys' and other's subsequent revisions (see Thys, 1968b; Trewavas, 1973, and p. 140 above). Certain species described after 1968 have been placed by their authors (Thys & Loiselle, 1971; Trewavas, 1973 & 1974; Roberts & Stewart, 1976; Stewart & Roberts, 1984) in one or other of these genera. *Pelmatochromis ansorgii* Blgr, the taxon of uncertain subgeneric affinity in Thys' (1968a) revision was chosen as the type species for a new genus described by Loiselle & Welcomme in 1972, and will be considered first.

THYSIA Loiselle & Welcomme, 1972

TYPE SPECIES. *Pelmatochromis ansorgii* Boulenger, 1901

SYNONYMY. *Pelmatochromis* (in part): Pellegrin, 1904 (*ansorgii* only); Boulenger, 1915 (*ansorgii*, *annectens* and *arnoldi*); Regan, 1922 (*ansorgii*, *annectens* and *arnoldi*); Thys, 1968a (*ansorgii* with which *arnoldi*, *annectens* and *maculifer* were synonymised).

Tilapia (in part): Ahl, 1939 (the species *maculifer*, see Thys, 1968a).

A description of the two *Thysia* species, *Thysia ansorgii* (Blgr) and *Th. annectens* (Blgr), together with extensive notes on their biology, is given by Loiselle & Welcomme (1972), although few anatomical details are discussed.

DIAGNOSIS. *Thysia* is distinguished from other African taxa by the following characters taken in combination. Body moderately deep, not fusiform (Fig. 12).

Neurocranial apophysis for the upper pharyngeal bones formed from the parasphenoid only (i.e. of the *Tilapia*-type; Fig. 13B) supraoccipital crest prominent; supraethmoid and vomer in contact.

Palatine with a two-point neurocranial contact, anteriorly through an articulation in the region of the ethmovomerine suture, and posteriorly with the ventral face of the lateral ethmoid (see Greenwood, 1985a); a calyx present between the metapterygoid and the hyomandibula.

A well-developed and circumscribed, visor-like hanging pad developed from the buccopharyngeal roof immediately anterior to the upper pharyngeal bones. Posterior facing margins of the major upper pharyngeal bones (the fused 3rd and 4th pharyngobranchials) forming a broad, shallow V, its apex directed anteriorly (Fig. 4A). No 'kukri'-shaped teeth on the lower pharyngeal bone (see p. 197 and Fig. 30), the teeth of which all have the tip of the major cusp pointing forwards

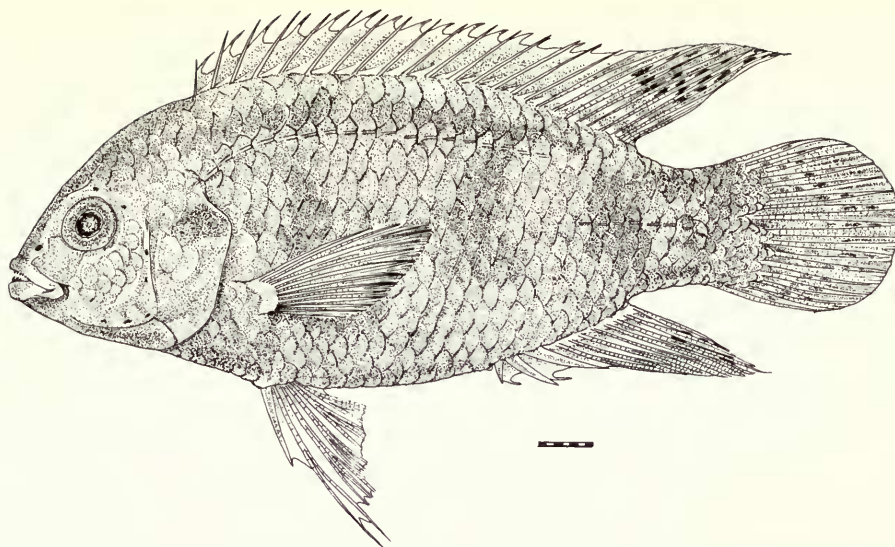


Fig. 12 *Thysia ansorgii*. One of the syntypes (BMNH 1901.1.28:9–12); scale bar in mms.
 Drawn by Gordon Howes.

and lying a little anterior to, or in the same vertical as the tooth's posterior margin. Anterior blade of the lower pharyngeal bone short, its length contained about 4 times in the overall length of the bone.

Infraorbital bones forming a complete lower and posterior margin to the orbit, the first infra-orbital (lachrymal) with 4 openings to its laterosensory canal.

Outer row jaw teeth, at least in specimens over 40 mm SL, unicuspid and with crowns of the compressed-conical type (see p. 158; Fig. 8); in fishes over 95 mm SL, a few (1–4) teeth situated anterolaterally in the lower jaw are aligned so that the crown points posteriorly, not buccally like the other teeth (see p. 158; Fig. 8).

Lower jaw less than 50 percent of head length. Anguloarticular with a roofed canal for the passage of the mandibulo-preopercular laterosensory canal.

Scales cycloid, 25–30 in the lateral-line series. Upper lateral-line clearly separated from the dorsal fin base over its entire length, and by $2\frac{1}{2}$ –3 scales at its highest point (i.e. the 8th or 9th pored scale in the series), and by one small and one large scale over the last 2–4 pored scales. Cheek almost entirely covered by 3 or 4 rows of scales, but with a small naked area anteroventrally. Chest scales not noticeably smaller than those situated anteroventrally on the flanks and belly; 16 scales around the caudal peduncle.

Gill-rakers on the ceratobranchial of the first arch pachydermatous, elongate and crescentic, orientated almost transversely across the arch, and closely applied to its surface; upper surface of the rakers tuberculate; distal tip produced and horn-like (see p. 160); 8–11 in number. A single row of dagger-like rakers on the upper part of the epibranchial. Microbranchiospines absent on all arches.

Total vertebral counts 25 or 26, comprising 13 abdominal and 12 or 13 caudal elements (the fused PU1 and U1 centra excluded from all counts). A single, well-developed supraneural (predorsal) bone is present.

Dorsal fin with 13–16 spines, anal with 3. Sexual dimorphism in the shape of the caudal fin margin, whose upper half projects further posteriorly in adult males than in females. Pelvic fin with the first ray longest in both sexes, and greatly produced in sexually active males. No *Tilapia*-spot; substrate guarder (Loiselle & Welcomme, 1972).

NOTES ON THE ANATOMY AND OTHER FEATURES. Anatomical and osteological studies were made on the type species, *Th. ansorgii* only, but comments on dental features include *Th. annectens* as well.

Like *Pelmatochromis*, most anatomical features in *Thysia* depart in no significant way from the modal condition in other African species.

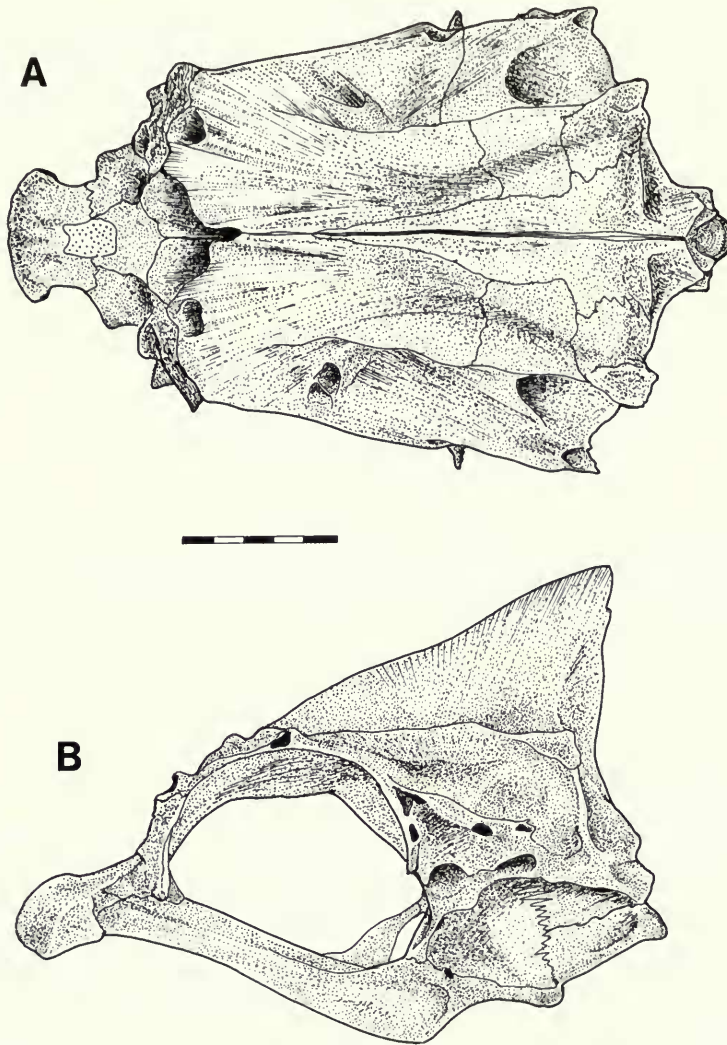


Fig. 13 Neurocranium of *Thysia ansorgii* in A. Dorsal; B. left lateral view. Scale bar in mm (BMNH 1977.11.8:430-455).

The neurocranium (Fig. 13) is generally similar to that in *Pelmatochromis buettikoferi* (p. 149). The supraoccipital crest is tall, the neurocranial apophysis for the upper pharyngeal bones is of the *Tilapia*-type, as is the lateral commissure (see Greenwood, 1986) but in *Thysia* there is no pre-commissural bridge although well-developed precommissural spurs are present on the prootic. The skull of *Thysia* differs, however, in having a slightly broader interorbital region (width contained about twice in the neurocranial length, as compared with $2\frac{1}{3}$ times in *P. buettikoferi*), and the anterior tip of the supraoccipital extends further forward to a point above the anterior third of the

orbit; also, the ethmovomerine skull region is a little shorter in *Thysia* than in *Pelmatochromis* ($3\frac{3}{4}$ times in neurocranial length cf. $3\frac{1}{4}$ times) and slopes less steeply (ca. 30° to the horizontal, cf. 50° in *P. buettikoferi*), and the supraethmoid is suturely united with the vomer.

The *infraorbital series* is complete, and the lachrymal has four openings to its laterosensory canal system. Somewhat more than the anterior third of the 2nd infraorbital overlaps the posterior shelf of the lachrymal (see Fig. 5E).

In the *pharyngobranchial skeleton*, the fourth epibranchial has a well-developed shank ridge which is almost spinous, and its quadrangular area is elongate and near-rectangular (see Greenwood, 1985a). There is a prominent and expansive cartilaginous extension from the anterior margin of the 2nd epibranchial; in one of the two specimens dissected the projection is almost square, in the other it is anvil-shaped.

The *upper pharyngeal bones*, and their arrangement, are similar to those in *Pelmatochromis*, and the lower bone closely resembles that of *P. buettikoferi* in its shape, proportions and dentition. In most respects the drawing of the lower pharyngeal bone in Loisélle & Welcomme (1972: fig. 4, which cf. Fig. 6B) is inaccurate, particularly with regard to the depiction of a deep median depression in the posterior margin, short and triangular articulating horns, and the somewhat 'waisted' appearance of the dentigerous surface.

The *vertebral column* is made up of 13 abdominal and 12 or 13 caudal vertebrae (the fused PU1 and U1 centra excluded); there is a single and slender supraneural bone.

No outstanding features were noted in the skeleton of the *caudal fin*. Likewise the *suspensorium*, *palatoquadrate arch* and the *jaw skeleton* show no obvious departure from the usual African cichlid condition. There is a well-developed calyx, open medially, formed from the metapterygoid and hyomandibular bones, and the palatine has a two-point articulation with the ethmovomerine region of the skull (see Greenwood, 1985a). In the preoperculum and the dentary there are, respectively, 7 and 5 openings to the laterosensory canals; the anguloarticular has a roofed passage for the mandibulo-preopercular canal.

Myology and arthrology of the jaws and palatoquadrate arch. Once again, there are no basic differences between *Thysia* and *Pelmatochromis*, although the relative sizes of certain muscles differ a little in the two taxa, and there is a smaller area of fusion between the A1 β and Aw tendons in *Thysia* (see p. 158). All in all, however, the conditions are those of the generalised African cichlid type.

Dorsal and ventral gill-arch musculature is essentially like that of *Pelmatochromis*, but in *Thysia* no part of the *levator posterior* muscle inserts on the articular horn of the lower pharyngeal bone, and the insertion of the *levator externus 4* muscle is merely a thin, tendinous thread. In the two latter characters *Thysia* shows the plesiomorphic condition for these muscles amongst cichlids, but it is not alone in so doing.

As in *Pelmatochromis* (and many other African cichlids; see Anker, 1978; Greenwood, 1985a) the *rectus ventralis* muscle inserts entirely on the semicircular ligament, whilst *obliquus ventralis 3* has the greater part inserted on the third hypobranchial, only a thin posterolateral section joining the ligament. The *transversus ventralis anterior* muscle is interrupted medially by the anterior blade of the lower pharyngeal bone.

Squamation. Between the highest point in the upper lateral-line (i.e. about the 8th and 9th pored scale) and the dorsal fin base there $2\frac{1}{2}$ or 3 scales, and between the last 2–4 pored scales and the fin there is one large and one very small scale. The chest is fully scaled, with the scales in that region not noticeably smaller than those on the venter. A small naked area occurs anteroventrally on the cheek which is otherwise fully scaled. As in the majority of African cichlids there are 16 scales around the caudal peduncle.

Fins. The lower rays in the upper half of the caudal fin are produced in adult males, with the result that the fin's posterior margin is irregular; in females, although the margin is regular, it is slightly extended around its midpoint.

In both sexes the first pelvic ray is the longest (albeit only slightly longer than the second ray in a few of the juveniles and adults examined). Adult males have the first ray greatly produced and filament-like (see fig. 1 in Loisélle & Welcomme, 1972).

Coloration. Loisélle & Welcomme (1972) give a detailed colour description, and there are good

colour photographs in Voss (1977; 1980) and Linke & Staeck (1981). A noteworthy feature in sexually active females is the presence of a prominent silver spot on the venter immediately above the ano-genital region.

Biology. Various aspects of *Thysia* biology, including its breeding behaviour and colour changes, are described by Loiselle & Welcomme (1972) and Voss (1977; 1980).

Relationships. The relationship of *Thysia* amongst the pelmatochromine fishes will be discussed in detail later (p. 191).

Its possible close relationship with *Hemichromis* and '*Pelmatochromis*' *thomasi* (now *Anomalochromis thomasi*; see Greenwood, 1985*b*) was suggested by Loiselle & Welcomme (1972); that idea is discussed, and discounted, in Greenwood (1985*a* & *b*).

In their paper Loiselle & Welcomme also argued that *Thysia* was not '... closely related to either the *Nanochromis*-*Pelvicachromis* complex or to *Chromidotilapia*', a conclusion very much at odds with that arrived at here (see p. 191). Several of the features in *Thysia* which Loiselle & Welcomme used in their argument (head shape, degree of jaw prostrusibility, position of the mouth, coloration) are not applicable to the question of overall relationship, but are concerned more with autapomorphic specialisations and thus with a low (e.g. generic or specific) level of classification. They do, however, comment on two characters (gill-raker morphology, and the pharyngeal pad) which I would consider to be of importance in establishing wider levels of interrelationship. Regarding gill-rakers, Loiselle & Welcomme (1972:54) indicate that those of *Chromidotilapia* differ from the rakers in *Thysia*, a conclusion with which I would not agree, especially since the feature they stress (tuberculation) is one most susceptible to the effects of preservation (p. 146). In my view, the overall gill-raker morphology, and indeed its more detailed aspects, are very similar in the two taxa, and can be considered as a unifying synapomorphy at the suprageneric level for these and other taxa (p. 191). Likewise, I do not agree with Loiselle & Welcomme's idea that, as compared with *Thysia* the hanging pad in *Nanochromis* is '... rudimentary' (*op.cit.*:55). Again, there is the possibility of preservation artefacts, but in none of the *Nanochromis* material I have examined would I describe the pad as rudimentary or in any way less well-developed than it is in *Thysia*.

CHROMIDOTILAPIA Boulenger, 1898

TYPE SPECIES: *Chromidotilapia kingsleyae* Boulenger, 1898 (by original designation).

SYNONYMY. *Pelmatochromis* (part): Pellegrin, 1904 (the species *kingsleyae*, *guntheri* and *pellegrini* [a junior synonym of *guntheri*; see Boulenger, 1915]); Boulenger, 1915 (*kingsleyae*, *guntheri*, and *nigrofasciatus* in part [the species *batesii*, treated as a synonym]); Regan, 1922 (the species included by Boulenger, 1915 above).

Pelmatochromis (*Chromidotilapia*) in part: Thys, 1968*a* (the species *guntheri*, *kingsleyae*, *batesii* and *schoutedeni*).

Chromidotilapia (part): Boulenger, 1898 (the species *kingsleyae* only); Trewavas, 1974 (*kingsleyae*, *guntheri* [with which *loennbergi* was included as a subspecies], and *finleyi*).

The genus *Chromidotilapia* was first described by Boulenger (1898) for his new species *kingsleyae*, (Fig. 14) although he did include, tentatively, another species, *C. frederici* (Castelnau). The latter, under a *nomen novum*, is now considered to be a *Serranochromis* (see Bell-Cross, 1975; Greenwood, 1979:304).

Interestingly, among the diagnostic features for *Chromidotilapia*, Boulenger (1898) noted that some of the lower jaw teeth had their unicuspid crowns directed posteriorly and not buccally, a feature now known to characterise all member taxa of the group II pelmatochromines (see p. 158).

Some six years after Boulenger erected this genus, Pellegrin (1904) synonymised it with *Pelmatochromis*, but gave no reasons for so doing. Regan (1922) followed Pellegrin, but again without comment or explanation. Thys (1968*a*), however, resurrected the taxon as, at least temporarily, a subgenus of *Pelmatochromis*.

With Thys' (1968*b*) inclusion of the nominate subgenus of *Pelmatochromis* in *Tilapia*, the subgenus *Chromidotilapia* regained its former generic status, at least by implication, and was formally confirmed therein by Trewavas (1974:388–389).

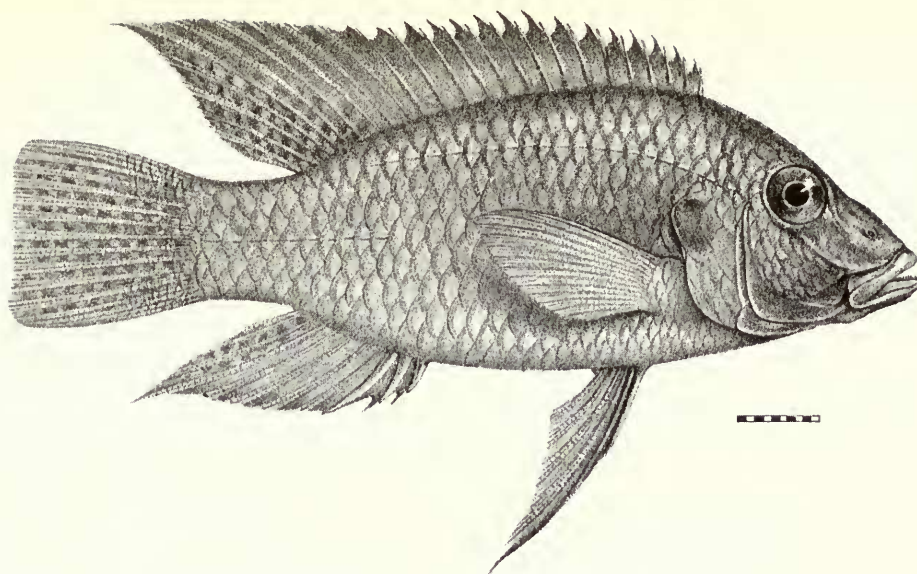


Fig. 14 *Chromidotilapia kingsleyae*. Holotype; from Boulenger, 1898. Scale bar in mms.

Thys' diagnosis for *Chromidotilapia* is based on (1) The well-developed hanging pad in the pharynx; (2) The broad and tuberculate gill-rakers in the outer row of the first gill-arch (which rakers he considered to have all tubercles of about the same size); (3) No sexual dimorphism in the shape of the caudal fin, which has a subtruncate posterior margin in both sexes; (4) The absence of microbranchiospines; (5) The first pelvic fin ray is the longest in both sexes.

Trewavas (1974) provided some data on intraspecific variability in gill-raker morphology, but did not comment on its relevance to Thys' diagnostic features for the genus, which she accepted without comment.

I have reservations about the significance and value of the gill-raker tuberculation character used by Thys since there is considerable interspecific and some intraspecific variability in this feature amongst the *Chromidotilapia* species I have examined. There is also the problem associated with *post-mortem* changes and with preservation induced variation (see p. 146).

Questions relating to autapomorphies and hence generic status amongst the pelmatochromines, especially those involving group II taxa, will be discussed later. For the moment it will suffice to note that none of those used by Thys can be considered autapomorphic for the genus.

Parentetically it should be noted here that Trewavas (1974:395) mentions a species, *C. caudifasciatus*, which she considers is close to *Chromidotilapia batesii*. Nowhere else in her paper does she mention *C. caudifasciatus*, and I can only assume that the reference is to the species *caudifasciatus* of Boulenger (1913), which Thys (1968a:367 and 380) included in his subgenus *Nanochromis* of *Pelmatochromis*. That species is considered later in this paper (p. 174), and certainly does not appear to be a *Chromidotilapia*.

DIAGNOSIS. As for *Thysia* (p. 160) except for: (1) Lachrymal with 5 openings to its laterosensory canal in all but one species (where there are 4). (2) Although posteriorly directed outer teeth occur anterolaterally in the lower jaw, their presence is apparently restricted to large individuals; it is not known at what size they first appear. Similarly, it is not known at what size the typical compressed-conical teeth are first present (see p. 158). (3) Lateral-line series with 25–29 scales; at its highest point (about the 8th scale) the upper lateral-line is separated from the dorsal fin base by two large and one very small scale, or by only two large scales. The last five or six pored scales are separated from the

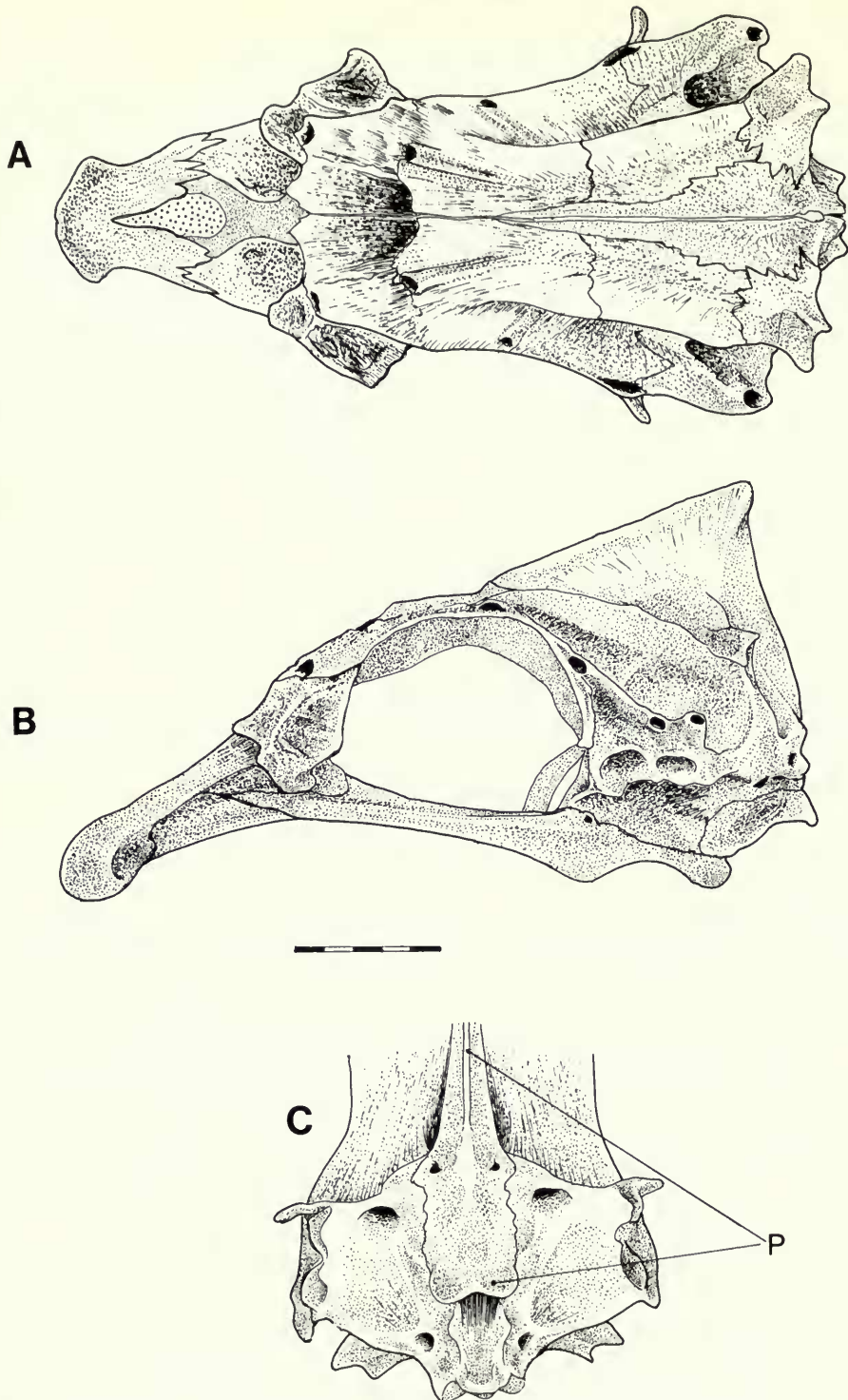


Fig. 15 Neurocranium of *Chromidotilapia kingsleyae* in: A. Dorsal; B. left lateral view. C. Neurocranial apophysis for the upper pharyngeal bones. P=parasphenoid. Scale bar in mms. (BMNH 1867.5.3:2).

fin base by one large and one very small scale. In some species the chest scales are slightly, but distinctly, smaller than those on the anteroventral aspects of the belly and flanks, but the size gradient between scales in the two regions is gradual; chest scales in other species as in *Thysia*. Cheek with 3 or 4 scale rows; in some species a narrow naked area anteroventrally. (4) Gill-rakers on the outer row of the first ceratobranchial are, in most species, more obtusely tuberculate than those in *Thysia*. (5) Caudal fin without any sexual dimorphism in the shape of its posterior margin, which varies from subtruncate to gently rounded. Dorsal fin with 14–17 spines, anal with 3. (6) Total vertebral count 24 or 25, comprising 12 (rare) —14 abdominal and 12 or 13 caudal centra (fused PU1 and U1 centra excluded). (7) Mouth brooder, at least during the later stages of brood care (see Myrberg, 1965; Thys, 1968a; Peters & Berns, 1978; Linke & Staake, 1981). (8) Adult females with an extensive metallic (silvery to coppery) flush on the dorsal fin; no silvery blotch above the vent in females.

NOTES ON THE ANATOMY AND OTHER FEATURES. Dissections and osteological studies were made on *C. kingsleyae*, *C. guntheri* and *C. finleyi*.

There is some intrageneric variation in the overall morphology of the *neurocranium* Figs 15–17).

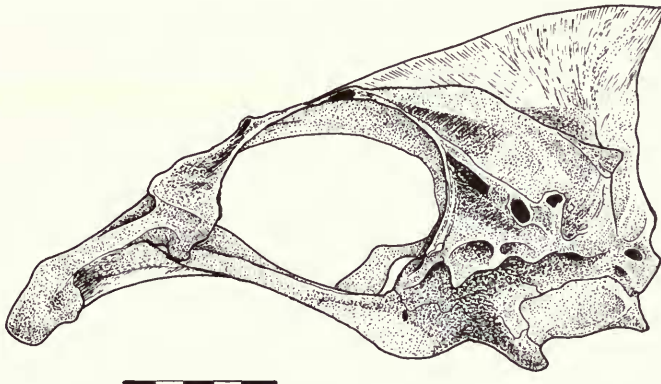


Fig. 16 Neurocranium of *Chromidotilapia guntheri loenbergi* in left lateral view. Scale bar in mms. (BMNH 1973.5.14:615–621).

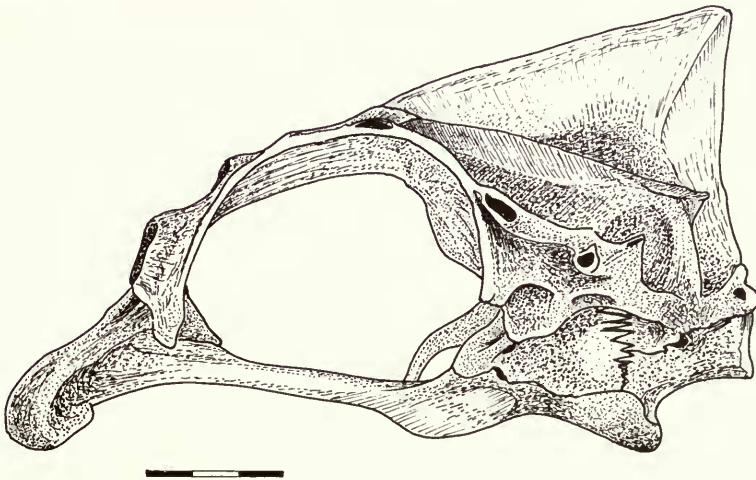


Fig. 17 Neurocranium of *Chromidotilapia finleyi* in left lateral view. Scale bar in mms. (BMNH 1973.5.14:544; one of the paratypes).

Chromidotilapia kingsleyae and *C. guntheri* have a more elongate and narrower skull than does *C. finleyi*; however, even in the comparatively foreshortened neurocranium of *C. finleyi*, the ethmovomerine region is relatively longer than in *Pelmatochromis* species (ca $3\frac{1}{2}$ times in neurocranial length cf. $3\frac{3}{4}$ times), and it is also somewhat narrower. This ethmovomerine attenuation is most extreme in *C. kingsleyae* and *C. guntheri*, where the region's length is contained about $2\frac{1}{2}$ to 3 times in neurocranial length. In both these species the ventral profile of the ethmovomerine skull region is noticeably elongate and decurved when compared with *Pelmatochromis*; even in *C. finleyi* the curvature and elongation is apparent. Skull width in *C. kingsleyae* and *C. guntheri* is less than in *C. finleyi* and *Pelmatochromis*. In all three *Chromidotilapia* species the supraethmoid and vomer are suturally united.

The *lateral commissure* can be of either the *Haplochromis*-type (*C. guntheri* and *C. finleyi*) or of an intermediate *Tilapia-Haplochromis* type in *C. kingsleyae*. A precommissural bridge is not developed in any species, but there are prominent precommissural spurs present ventrally on the prootic, and less obvious ones dorsally on that bone (Greenwood, 1986).

The *infraorbital series* (Fig. 5B) is complete. About two-thirds of the second infraorbital bone overlaps the posteriorly directed shelf of the lachrymal. The latter bone has a characteristic apron-like shape in all three species; its overall proportions are clearly rectangular in *C. kingsleyae* and *C. guntheri*, but are more nearly square in *C. finleyi*. The latter species also differs in having only four and not five openings to its laterosensory canal. Four openings are the commonest condition amongst pelmatochromines, and are thought to represent the plesiomorphic state in cichlids (see Trewavas, 1983; Oliver, 1984; Greenwood, 1985a).

In the *vertebral column* there are 12 (rarely) to 14 abdominal vertebrae (mode 13), and 12 (mode) or 13 caudal elements (excluding the fused PU1 and U1 centra), giving a total count of 24 (rare) to 26. In the two skeletons of *C. kingsleyae* available, and in the single skeleton of *C. batesii*, there is a strong and deep spondylophysal apophysis on the third abdominal centrum.

The *myology, arthrology and osteology of the jaws and pharyngobranchial region* in *Chromidotilapia* are, with few minor exceptions, like those in *Thysia* (see p. 163). The dorsal gill-arch musculature, examined in *C. guntheri* and *C. finleyi*, however, is more like that of *Pelmatochromis* than *Thysia* since there is a small musculose, rather than tendinous, slip of the fourth *levator externus* muscle inserting onto the fourth epibranchial, and a musculose attachment of the *levator posterior* muscle to the horn of the lower pharyngeal bone. In those respects, *Chromidotilapia* is more derived than is *Thysia*.

Due to inadequate material, little could be learnt about the extent to which the anterior cartilaginous flange on the *second epibranchial* is developed. In *C. finleyi* the flange is large and rectangular in outline. Judging from the available skeletal material the *pharyngobranchial skeleton* in *Chromidotilapia* shows no outstanding features (see also Greenwood, 1985a).

In the lower jaw, the tendon A1 β of the *adductor mandibulae* I muscle is completely free from that of the Aw tendon, the usual condition in cichlids.

The ascending process of the premaxilla is, relative to the alveolar arm of the bone, longer in *Chromidotilapia* than in *Thysia*, and markedly longer than in *Pelmatochromis*.

The *dentition* in adult specimens of all species examined has both the compressed-conical unicuspid teeth typical of group II pelmatochromines, and the equally typical posteriorly directed anterolateral teeth in the dentary (see p. 158). Smaller fishes, however, have outer row teeth of a slightly different kind. In these, the crown has a less obviously flattened labial surface and consequently has less distinct sharp-edged margins to the crown. Smaller specimens also lack the posteriorly directed anterolateral dentary teeth. Furthermore, some 'shadow-shouldered' teeth or even distinctly 'shouldered' teeth (see p. 145) are present in both jaws, at least in specimens of *C. kingsleyae* less than 60 mm SL, and in *C. finleyi* of less than 50 mm SL. In both these species the figures given refer to the largest of the 'small' specimens available for study in which such teeth were observed, and thus may not truly reflect the minimum sizes above which a fully 'adult' dentition is present. Posteriorly directed anterolateral teeth are absent in the dentary of most *C. kingsleyae* specimens less than 50 mm SL, but are present in one fish of only 40 mm SL. The size range of the samples from which these data were derived are 31–74 mm SL, and 29–46 mm SL for *C. kingsleyae* and *C. finleyi* respectively.

As in *Thysia*, the first pelvic fin ray is the longest, and is greatly produced in adult males. Unlike *Thysia*, there is no sexual dimorphism in the shape of the caudal fin margin which, in *Chromidotilapia*, ranges from subtruncate to gently rounded.

Coloration. As far as I can tell from the literature, especially the excellent colour photographs in Linke & Staeck (1981), all known species of *Chromidotilapia* have an unusual form of sexually dimorphic coloration. That is, an extensive metallic sheen, ranging from coppery to silver in colour, on the dorsal fin of sexually active females. Although a metallic band is developed on the dorsal fin of adult females in many *Pelvicachromis* species, it is, in these, far less extensive an area, and is a much more clearly defined band than is the case in *Chromidotilapia*. Again, judging from the literature, the *Chromidotilapia*-type of female dorsal fin colouring has not been recorded in other taxa of African cichlids, but our knowledge of live colours in these fishes is extremely limited. A possible exception, for example, may be *Nanochromis caudifasciatus* (see p. 174 for its new generic placement); in Linke & Staeck's (1981) figure of that species there is seemingly a silvery sheen on the female's dorsal fin which closely approximates to that of *Chromidotilapia* in area and appearance. In at least one species (*C. finleyi*, Trewavas, 1974) young fishes have a spot on the dorsal fin closely resembling a *Tilapia*-spot.

Breeding habits. *Chromidotilapia* is unique amongst the pelmatochromines in being a mouth-brooder. The breeding biology of *C. guntheri* is described in some detail by Myrberg (1965), there are general accounts of other species in Linke & Staeck (1981), and the mouth-brooding habits of *C. batesii* and *C. guntheri* are reviewed in the broad context of the cichlids as a whole by Peters & Berns (1978).

Included species. It is clear from the literature (Thys, 1968a; Trewavas, 1974 and personal communications; Linke & Staeck, 1981), that species level taxonomy for *Chromidotilapia* is in a very unsatisfactory state. Currently, seven nominal species are recognised, viz.: *C. kingsleyae* Blgr. 1898; *C. guntheri* (Sauvage), 1882, with two subspecies (see Trewavas, 1974), *C. batesii* (Blgr), 1901; *C. finleyi* Trewavas, 1974; *C. linkei*, Staeck, 1980; *C. schoutedeni* (Poll & Thys), 1967, and *C. busumtwensis* Paulo, 1979. It seems very likely from Linke & Staeck's (1981) account of supposedly intraspecific colour variation, that a number of sibling species probably have yet to be recognised and described.

Trewavas (cited by Linke & Staeck [1981:89] as a personal communication) has suggested that *Pelvicachromis humilis* (Blgr), 1916 may be closely related to, if not actually a member of, *Chromidotilapia*. Certainly the general facies of that species are distinctive amongst the other *Pelvicachromis*, and do resemble those of *Chromidotilapia*. However, *P. humilis* does not share with *Chromidotilapia* any of the critical autapomorphies defining that genus, but it does share with other *Pelvicachromis* species the apomorphic features of that taxon (see. p. 174).

PELVICACHROMIS Thys van den Audenaerde, 1968

TYPE SPECIES. *Pelmatochromis pulcher* Boulenger, 1901 (by original designation).

SYNONYMY. *Pelmatochromis* (part): Pellegrin, 1904 (the species *pulcher*, *subocellatus* and *taeniatus*); Boulenger, 1915 (the species *pulcher*, *kribensis*, *subocellatus* and *taeniatus*); Boulenger, 1916 (the species *humilis*); Regan, 1922 (as for Boulenger, 1915 and 1916).

Pelmatochromis (*Pelvicachromis*): Thys, 1968a (the species *pulcher*, *humilis*, *roloffii*, *subocellatus*, *taeniatus* [with which is synonymised *kribensis*], and a number of informally named taxa).

Like the other subgenera defined by Thys (1968a), *Pelvicachromis* was raised to generic rank by his referral (Thys, 1968b) of the nominate subgenus of *Pelmatochromis* to *Tilapia*, and by Trewavas' (1974) subsequent recognition of that subgenus as a full genus.

Thys (1968a) defined and diagnosed *Pelvicachromis* on a single feature, the unusual sexual dimorphism exhibited by the pelvic fins. In *Pelvicachromis* females the second or third branched pelvic ray is the longest, thereby giving the fin a distinctly rounded apex to its distal margin; in males, the first pelvic ray is clearly the longest and is often further produced in sexually active males.

Judging from extra- and intrafamilial out-group comparisons, this characteristic should be treated as an autapomorphy for the genus. However, it is closely approached by most, if not all

species of *Nanochromis* (*sensu* Thys, 1968a; but see below where the taxon is subdivided into two related genera). Pelvic fins in which the second and third rays are the longest also occur in at least one other African lineage, *Orthochromis* (Greenwood, 1979:297). In *Orthochromis*, however, this fin character is congruent with other apomorphies which would not indicate a close phyletic relationship with either *Pelvicachromis* or *Nanochromis*; furthermore, in *Orthochromis* the shape of the pelvic fins is identical in both sexes. As note above, in *Nanochromis*, as in *Pelvicachromis*, the fin is sexually dimorphic, but, unlike *Pelvicachromis*, *Nanochromis* females have the second ray only very slightly longer than the first; despite that, the apex of the fin's distal margin has a rounded rather than a pointed appearance. Again, there are congruent apomorphic features which indicate that *Nanochromis* is a distinct lineage.

At least as far as morphological features are concerned, the characteristic pelvic fin dimorphism of *Pelvicachromis* would seem to be the sole autapomorphic feature for the genus. That character, combined with the rather steeply decurved dorsal head profile, the short snout and the relatively elongate body-form in all species, make *Pelvicachromis* an easily recognisable member of the pelmatochromine group.

DIAGNOSIS. *Pelvicachromis* is distinguished from other genera of African cichlid fishes by the following characters taken in combination: Body form relatively elongate and moderately compressed, dorsal head profile decurved (Fig. 18).

Neurocranial apophysis for the upper pharyngeal bones usually of the *Tilapia*-type, that is formed from the parasphenoid only, but in at least some individuals of one species it is of the *Tropheus*-type, with small contributions from the basioccipital bones (see Greenwood, 1978). Supraoccipital crest relatively low, and not rising to a high peak posteriorly (Fig. 19). Supraethmoid and vomer in contact in at least two species. Palatine bone with a two-point neurocranial contact, anteriorly with an articulation in the region of the ethmovomerine suture, and posteriorly with a facet on the ventral face of the lateral ethmoid.

A visor-like, clearly circumscribed hanging pad anterior to the upper pharyngeal bones. Posterior facing margins of the major upper pharyngeal bones (the fused 3rd and 4th pharyngo-branchials of each side) aligned so as to form a broad and shallow V with an anteriorly directed apex. No 'kukri'-shaped teeth (see p. 197) on the lower pharyngeal bone. Anterior blade of the lower pharyngeal bone short, contained 3–4 times in the overall length of the bone.

Infraorbital series of bones complete, the first infraorbital (lachrymal) usually with four openings to its laterosensory canal, but possibly in some species (or individuals) with five openings (see p. 171).

Outer row teeth in both jaws unicuspid and of the compressed-conical type (see p. 158), some teeth situated anterolaterally in the dentary have the cusp directed posteriorly and not buccally (Figs 8 & 9). Inner row teeth arranged in 1–3 rows, unicuspid or with weak and bilateral shoulders.

Lower jaw length less than 50 percent of head length. Premaxillary ascending processes as long as, slightly longer or slightly shorter than the alveolar arms. Anguloarticular with a roofed passage for the mandibulo-preopercular laterosensory canal. Mouth horizontal or very slightly inclined.

Scales cycloid. 25–30 in the lateral-line series; lateral-line clearly separated from the dorsal fin base over its entire length, by $1\frac{1}{2}$ or two scales at its highest point (above the 8th or 9th pored scales) and by one large and one very small scale above the last 4–6 pored scales. Cheek with 2 (rare) or 3 rows of scales; a small naked area anteroventrally sometimes present. Chest scales distinctly smaller than those on the belly and anteroventral aspects of the flanks, the size intergradation being rather abrupt. Sixteen scales around the caudal peduncle.

Gill-rakers of the outer row on the first ceratobranchial long, pachydermatous and crescentic, aligned transversely and close to the arch, the concave upper face variously tuberculate, the distal tip produced and horn-like; 9–12 in number. Epibranchial rakers of the first arch slender and flattened, sword- or dagger-shaped, arranged in a single row except near the epi-ceratobranchial junction. Microbranchiospines are absent.

Abdominal vertebrae 13–15 (mode 14) in number, caudal elements 10–12 (mode 12), giving total counts of 23–27 (all counts exclude the fused P_{U1} and U₁ centra).

A single, well-developed supraneural (predorsal) bone. Dorsal fin with 14–16 spines, anal with 3.

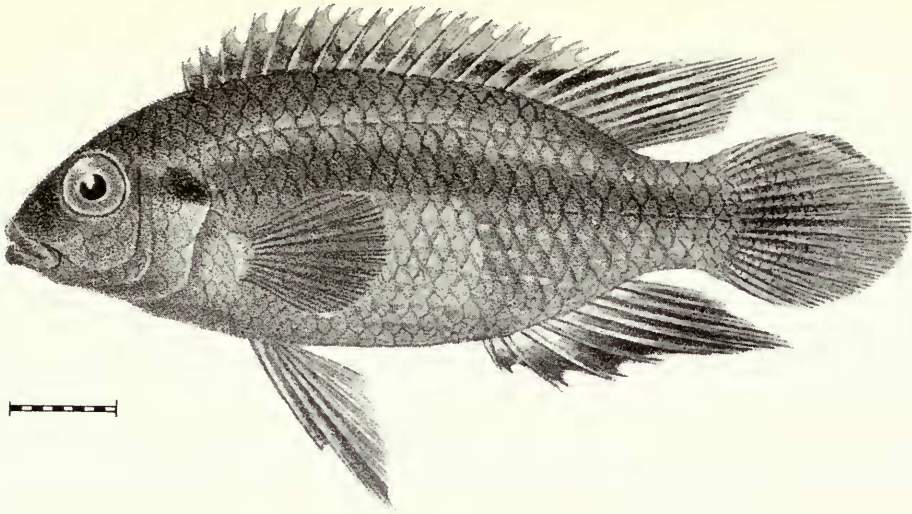


Fig. 18 *Pelvicachromis pulcher*, one of the types. From Boulenger (1901); *Proceedings of the Zoological Society of London*. Scale bar in mms.

Caudal fin rounded, but showing sexual dimorphism in some species where males have the median rays, or the lower rays of the upper lobe, produced. Pelvic fins sexually dimorphic; females with the second ray (sometimes both the 2nd and 3rd rays) longer than the first ray, thus producing a rounded apex to the fin's distal margin; in males the first ray is noticeably the longest, and the fin has a pointed apex.

Body coloration in breeding individuals with a marked sexual dimorphism. No true *Tilapia*-spot, but in some species the females have a dark spot approximately in the position of the *Tilapia*-spot.

Apparently all species are cave spawners and breeders.

NOTES ON THE ANATOMY AND OTHER FEATURES. In its overall morphology, the *neurocranium* in *Pelvicachromis pulcher*, *P. subocellatus* and *P. taeniatus* (the only species for which adequate study material was available) closely approximates to that of *Pelmatochromis buettikoferi* (cf. Figs 3 & 19). The supraoccipital crest, however, is much lower and slopes gently rather than steeply. The fronto-parietal crests in the *Pelvicachromis* species examined are better developed than in *P. buettikoferi*, and unlike that species, the vomer and supraethmoid are suturally united in *Pelvicachromis*, which thus shows the common African cichlid condition. In both genera the ethmovomerine region of the skull is short (ca. $3\frac{1}{4}$ - $3\frac{1}{2}$ times in neurocranial length) and slopes upwards fairly steeply at an angle of about 50° to the horizontal.

The available neurocrania of *Pelvicachromis pulcher* and *P. taeniatus* have a typical *Tilapia*-type apophysis for the upper pharyngeal bones, but in the single *P. subocellatus* examined there is, bilaterally, a very small contribution by the basioccipital, the apophysis thus closely resembling the *Tropheus*-type (Greenwood, 1978).

In all three species the lateral commissure is of the *Haplochromis*-type, and a well-developed precommissural bridge is present in *P. pulcher* and *P. subocellatus*, but is absent in *P. taeniatus*, as are any indications of precommissural spurs on the prootic (see Greenwood, 1986).

The *infraorbital bone series* is complete (Fig. 5D). The first bone (lachrymal) has four openings to its laterosensory canal system; almost half of the second bone overlaps the posteriorly directed flange on the lachrymal. Trewavas (1983) records that some (but unnamed) *Pelvicachromis* species are variable with respect to the number of openings in the lachrymal laterosensory canal system,

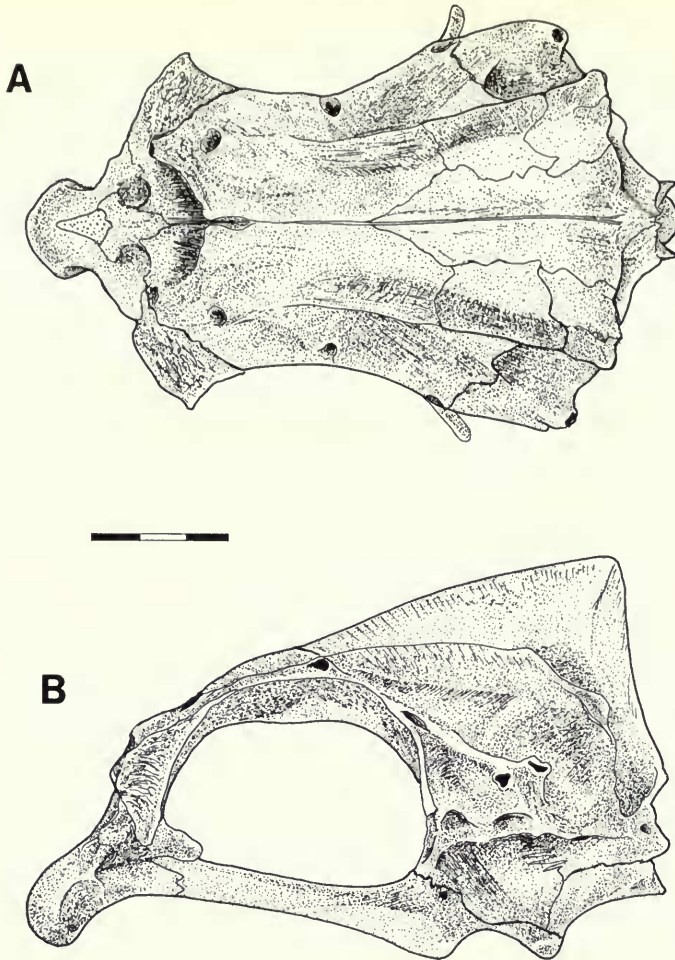


Fig. 19 Neurocranium of *Pelvicachromis pulcher* in: A. Dorsal, and B. Left lateral view; the basisphenoid bone is missing in this specimen. Scale bar in mms (BMNH 1901.1.28:13-20).

having either 4 or 5; that situation was not encountered in any of the species or specimens I examined.

The *vertebral column* is composed of 23-26 vertebrae (excluding the fused PU1 and U1 centra), comprising 13 or 14 (mode) abdominal and 10-12 (mode) caudal elements (figures obtained from radiographs of four species, viz: *P. pulcher* type series; *P. taeniatus* holotype and one other specimen, and specimens identified as *P. subocellatus* and *P. roloffi*). Counts were also obtained from radiographs of *P. humilis* holotype, and are noticeable for the higher number (15) of abdominal centra (total count 27); the taxonomic status of *P. humilis* is discussed later (p. 174).

A single supraneural (predorsal) bone is present in all the species and specimens radiographed.

In *other osteological features* examined the skeleton of *Pelvicachromis* showed no seemingly significant differences from that of the other pelmatochromines considered so far. The *pharyngo-branchial skeleton*, for example, is like that in *Pelmatochromis*, as is the lay-out of its pharyngeal bones. There is an expansive cartilaginous projection from the anterior margin of the second epibranchial bone (as in *Pelmatochromis*), although the shank ridge on the fourth epibranchial is better defined and spine-like in *Pelvicachromis* (see p. 151). The lower pharyngeal bone and its dentition are similar in both genera (see Fig. 6).

The *gill-rakers* show some interspecific variation in the extent to which the upper surface is tuberculated, and in the extent to which the median membrane is developed between the inner and outer raker series on the first ceratobranchial. However, possible differences in the quality of preservation (and the length of time in preservative) render difficult any assessment of the significance that can be attached to these differences. Be that as it may, the rakers in all the species examined are clearly of the derived pelmatochromine type discussed on p. 159.

Myology and arthrology. Only *P. pulcher*, *P. subocellatus* and *P. roloffi* have been dissected. In none does the myology or the arthrology of the jaws show any outstanding features. Both are essentially of the type described for *Pelmatochromis* (p. 153), except that, as in most African species dissected, there is no fusion between the tendons $A1\beta$ and A_w in the *adductor mandibulae* series.

Likewise, the dorsal pharyngobranchial musculature is like that of *Pelmatochromis*, and is thus of the basic cichlid type. Ventrally, and unlike the other pelmatochromines discussed so far, the *obliquus ventralis* 3 muscle in *P. pulcher* and *P. subocellatus* has no insertion on the semi-circular ligament, but inserts entirely on the third hypobranchial. *Pelvicachromis roloffi*, on the other hand, has a few fibres of the muscle attaching to the ligament, as is the case in the other pelmatochromines.

All three species have the typical African cichlid condition of the *transversus ventralis anterior* muscle being interrupted medially by the anterior blade of the lower pharyngeal bone (see Stiassny, 1982).

Squamation. Little need be added to the details given in the diagnosis (p. 170), except to note that there are few scales between the highest point of the upper lateral-line and the dorsal fin base, namely $1\frac{1}{2}$ or 2, and a single scale, or one large and one very small scale, between the fin base and the last 4–6 pored upper lateral-line scales.

Chest scales in *Pelvicachromis* are distinctly smaller than those on the belly and anteroventral aspects of the flanks, and there is a fairly abrupt change in size between these scales and those on the chest. The degree of abruptness shows some interspecific variation.

Fins. The nature of the sexual dimorphism in the pelvic fins was noted above (p. 169), where the differences between *Pelvicachromis* and members of the *Nanochromis* group (*sensu* Thys, 1968a) were also discussed. The phyletic significance of those similarities, and differences, will be considered later (p. 194).

As Thys (1968a:357;399) noted, there are two distinct but sympatric groups of *Pelvicachromis* species. In one there is an obvious sexual dimorphism in caudal fin shape, with males having the central caudal fin rays (or the lower few rays in the upper lobe of the fin) somewhat extended so as to disrupt the outline of an otherwise rounded-subtruncate to clearly rounded margin (the latter being the usual female condition). The second group shows no sexual dimorphism in caudal fin outline, which is either rounded or rounded-subtruncate in both sexes.

Dentition. In the *Pelvicachromis* species I have examined, the dentition is typically that of all group II pelmatochromine taxa (see p. 158). It has proved impossible to determine at what size the anterolateral, backward-pointing teeth appear in the dentary, or to gather any information on the nature of the teeth in small specimens.

Inner row teeth of both jaws are always slender and somewhat smaller than those of the outer row, and show a variety of crown shapes; some have simple attenuated-conical crowns, others are very similar to the compressed-conical teeth of the outer row, or may have compressed-conical crowns with faint traces of shoulders flanking the tip bilaterally. Again, because of insufficient material covering small specimens, it is impossible to tell if there are size correlated changes in the nature of the inner teeth.

Coloration. A true *Tilapia*-spot has not been recorded in any *Pelvicachromis* species, and it has yet to be discovered whether or not the similarly placed ocellus (or conjoined ocelli) which occur in the adult females of some species is the homologue of a *Tilapia*-spot (see colour figures, pages 91, 115 & 118 in Linke & Staeck, 1981).

Breeding. All the species whose breeding behaviour is known are substrate spawners and guarders, often using holes and small cave-like irregularities of the bottom (Linke & Staeck, 1981: 82–87). Aquarist literature relating to this genus can be misleading since there are considerable difficulties involved in species identification, and because several 'trade' binomia have been con-

cocted by dealers (see Thys, 1968a). However, the accounts given by Linke & Staeck (1981) are both critical and carefully researched, and provide a good summary of *Pelvicachromis* breeding biology.

Included species. Species level taxonomy for *Pelvicachromis* is in a far from satisfactory state, as Thys (1968a) clearly showed in his critical review of the genus. Currently, *P. pulcher* (Blgr) 1901, *P. humilis* (Blgr) 1916, *P. roloffii* (Thys) 1968, *P. taeniatus* (Blgr) 1901 and *P. subocellatus* (Gnthr) 1871 are recognised, together with a number of informally designated 'forms' discussed by Thys (1968a), and by Linke & Staeck (1981); for detailed synonymies of these species reference should be made to both those publications.

Uncertainties about the correct generic placement of *Pelvicachromis humilis* were noted above (p. 169) in connection with Trewavas' suggestion (pers. comm., mentioned by Linke & Staeck, 1981) that the species could be a member of the *Chromidotilapia* lineage.

Certainly in its general facies *P. humilis* does approach the *Chromidotilapia* type, particularly in having a straight and sloping dorsal head profile rather than a rounded, decurved one. It also differs in certain osteological characters from the modal *Pelvicachromis* condition; the supra-occipital crest is lower, the ethmovomerine skull region is slightly longer and slopes at a somewhat lower angle (ca. 40° cf. 50° to the horizontal), the interorbital region is narrower, and the vertebral count (27) is higher as a consequence of there being 15 rather than 13 or 14 abdominal centra.

However, in other anatomical and osteological features, *P. humilis* shows nothing which would suggest that it is more closely related to *Chromidotilapia* than to *Pelvicachromis*.

Since *P. humilis* apparently shares none of the autapomorphic features characterising *Chromidotilapia* (it is not, for instance, a mouth-brooder), it would seem best to treat it, for the time being, as a somewhat atypical member of the genus *Pelvicachromis*. Its relationships within that genus may be clarified when a detailed and wide-ranging species-level revision of *Pelvicachromis* has been carried out.

Parenthetically, note can be made of what seems to be an individual aberrancy in one of the two *P. humilis* specimens I have dissected. In that fish, besides the *adductor mandibulae* 1 muscle having a tendon to the maxilla, and its ventrally directed A1 β tendon to the lower jaw, there is a third and short tendon linking the head of the muscle with the coronoid process of the anguloarticular bone (Fig. 20). The second specimen examined has the usual two-tendon arrangement.

PARANANOCHROMIS gen. nov.

TYPE SPECIES: *Pelmatochromis longirostris* Boulenger, 1903.

SYNONYMY. *Pelmatochromis* (part): Pellegrin, 1904 (the species *longirostris* only); Boulenger, 1915 (the species *longirostris* and *caudifasciatus*).

Pelmatochromis (*Nanochromis*) in part: Thys, 1968a (the species *longirostris* and *caudifasciatus*)

Nanochromis (part): Trewavas, 1975 (the species *gabonicus*)

Thys (1968a:379–381) included *Pelmatochromis longirostris* and *P. caudifasciatus* in his subgenus *Nanochromis* (a taxon originally described and ranked as a genus by Pellegrin, 1904). Thys' reasons for so placing these two species was that, unlike most of the other pelmatochromines he dealt with, but like the species he referred to *Nanochromis*, both *P. longirostris* and *P. caudifasciatus* have only 12 (and not 16) scales around the caudal peduncle. He also expressed the belief that these two species, together with certain unnamed material '... seem to constitute a continuous evolutionary line' with *Nanochromis nudiceps* (the type species of Pellegrin's genus).

At the time Thys' paper was published (1968), *Nanochromis* (*sensu* Pellegrin) was rather poorly defined, the chief character given to distinguish it from *Pelmatochromis* (*sensu* Regan, 1922) being the extreme dorsad position of the upper lateral-line; Regan (*op.cit.*) diagnosed the genus on the basis of its having the 'Upper lateral line contiguous to dorsal fin', a slightly inaccurate description since almost the anterior half of that line is separated from the dorsal fin base by at least 1 scale row.

Thys (1968a) expressed doubts about the validity of the lateral line position as '... a good generic character' but did not elaborate further on that point, nor on what a 'good' generic character might be. He also expressed some misgivings about the significance of the reduced circumpeduncular

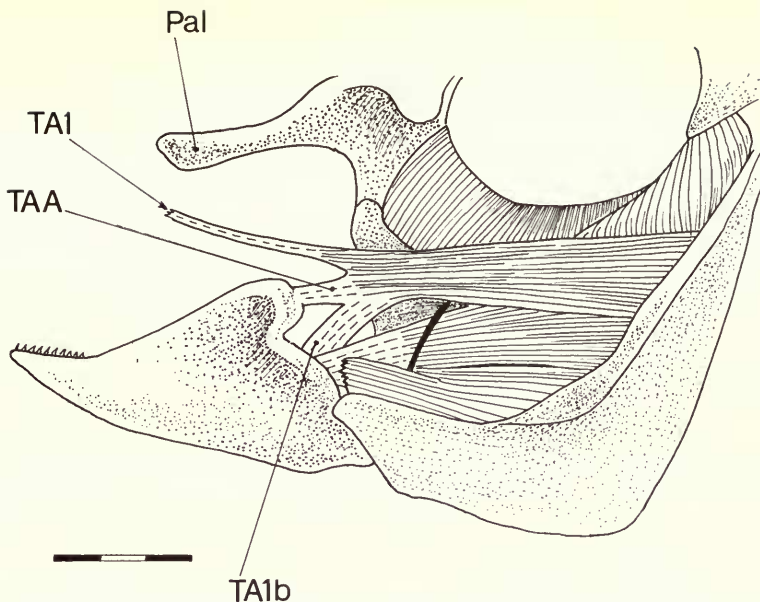


Fig. 20 An unusual arrangement of the tendons associated with the *adductor mandibulae* 1 muscle in an aberrant specimen of *Pelvicachromis humilis* (BMNH 1972.3.16:8–10). Left lateral view. Scale bar in mms. Pal = palatine bone; TAI = maxillary tendon of the first adductor muscle; TAA = anomalous tendon inserting on the anguloarticular bone; TA1b = tendon from first adductor muscle to the lower jaw.

scale count since, although uncommon amongst African cichlids (where 16 scales are usual), it does occur in a few other species which, because of this feature, he had not assigned to a particular genus or subgenus.

Nevertheless, and presumably because *caudifasciatus* and *longirostris* fell into what he considered 'a continuous evolutionary line', Thys included the two species, with those of *Nanochromis*, as a distinct subdivision (i.e. subgenus) of *Pelmatochromis*.

In a phylogenetic context, I cannot agree with Thys on the supposed insignificance of the lateral-line position in *Nanochromis* (see p. 183), the more so since in that genus (*sensu* Pellegrin) it is congruent with other apomorphic features recently noted by Stewart and Roberts (1984). In my view, the partial but extreme contiguity of the dorsal fin base and the upper lateral-line, together with the other synapomorphic features in *Nanochromis* (especially the nature of the infraorbital bone series; see p. 181) indicate an *immediate* common ancestor for the species showing them. That ancestor was not shared by *longirostris* and *caudifasciatus* (or by the species *gabonicus* of Trewavas, 1975; see synonymy above), all taxa in which the *Nanochromis* synapomorphies are not present.

However, *Parananochromis* (which I have erected for the three latter species) and *Nanochromis* (*sensu* Pellegrin) do share, uniquely amongst the pelmatochromines, two apomorphic characters, namely 12 scales around the caudal peduncle, and a *Haplochromis*-type neurocranial apophysis for the upper pharyngeal bones (the latter a feature not noticed by Regan [1922], Thys [1968a], or Trewavas [1975]).

On the basis of those synapomorphies I would postulate a more distant, but still close, common ancestry for the two genera. It might be argued that the relationship of the lineages could best be indicated by ranking them as subgenera of *Nanochromis*. I would agree with that argument but for the possibility of future research showing the existence of two lineages within *Nanochromis* as presently construed (see p. 187). For that reason I prefer to treat *Parananochromis* as a genus, and rely on a cladogram (Fig. 29) to show its sister-group relationship with *Nanochromis*. In the sense that *Nanochromis* and *Parananochromis* are sister taxa, I would agree with Thys' idea that together

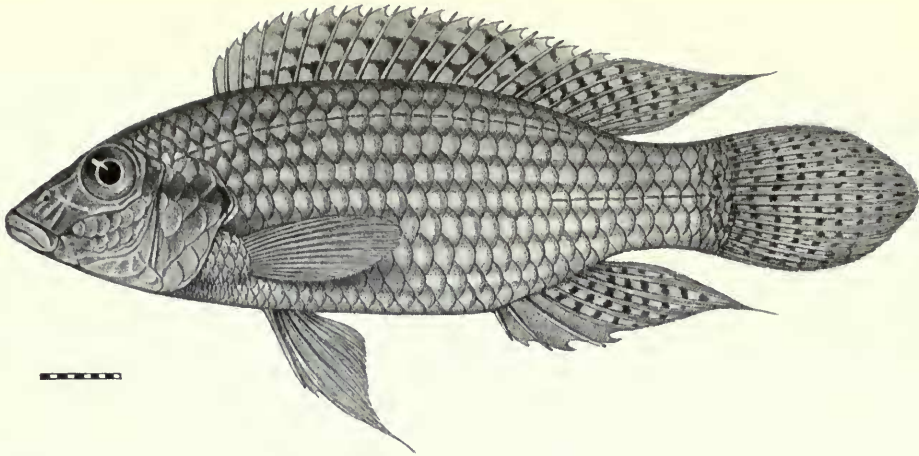


Fig. 21 *Parananochromis longirostris*; holotype. From the original drawing by J. Green. Scale bar in mms.

they form a continuous evolutionary line, with *Nanochromis* representing the more derived portion of the lineage.

Thys (1968a) notes that in the species he referred to his subgenus *Nanochromis* there is '... a feebly developed or even no hanging pad in the roof of the pharynx' and that the ventral fins are rounded in both sexes. The species which I have examined, and which I place in *Parananochromis*, all have, *pace* Thys, a well-developed and typically circumscribed, visor-like hanging pad, and although the pelvic fins are distinctly or almost rounded in females, they are pointed in males.

Thys & Loisel (1971) described two new *Nanochromis* species (*sensu* Thys, 1968a), *N. robertsi* and *N. cavalliensis*. Superficially, both seemingly would belong to *Parananochromis* since neither shows the defining features of *Nanochromis* (*sensu* Pellegrin, see p. 181). However, in both species the neurocranial apophysis for the upper pharyngeal bones is of the *Tilapia*-type, and both have 13 or 14 scales around the caudal peduncle (cf. 12 in *Parananochromis* and *Nanochromis*, and 16 in other group II pelmatochromines). On those grounds I exclude *robertsi* and *cavalliensis* from both *Parananochromis* and *Nanochromis* (see p. 188).

DIAGNOSIS. *Parananochromis* is distinguished from other genera of African cichlids by the following characters taken in combination: Body form moderately elongate and compressed; dorsal head profile sloping steeply but somewhat decurved (Fig. 21).

Neurocranial apophysis for the upper pharyngeal bones of the *Haplochromis*-type, with substantial contributions from the basioccipital. Supraethmoid not contacting the vomer in the one species examined (*P. longirostris*). Supraoccipital crest relatively low, and not rising to a high peak posteriorly. Palatine with a two-point neurocranial contact, anteriorly through an articulation in the region of the ethmovomerine suture, and posteriorly with the ventral face of the lateral ethmoid (see Greenwood, 1985a). A calyx is developed between the metapterygoid and the hyomandibula.

Infraorbital bone series complete, the first infraorbital (lachrymal) with four openings to its laterosensory canal (Fig. 5C).

Lower jaw length less than 50 percent of the head length; anguloarticular with a roofed canal for the passage of the mandibulo-preopercular laterosensory canal.

Outer row jaw teeth of the typical group II pelmatochromine type (see p. 158); inner row teeth unicuspid, arranged in from 1–3 rows.

A well-developed and clearly circumscribed, visor-like hanging pad developed from the pharyngeal roof immediately anterior to the upper pharyngeal bones. Posterior facing margins of the fused 3rd and 4th pharyngobranchials aligned so as to form a broad and shallow V, its apex

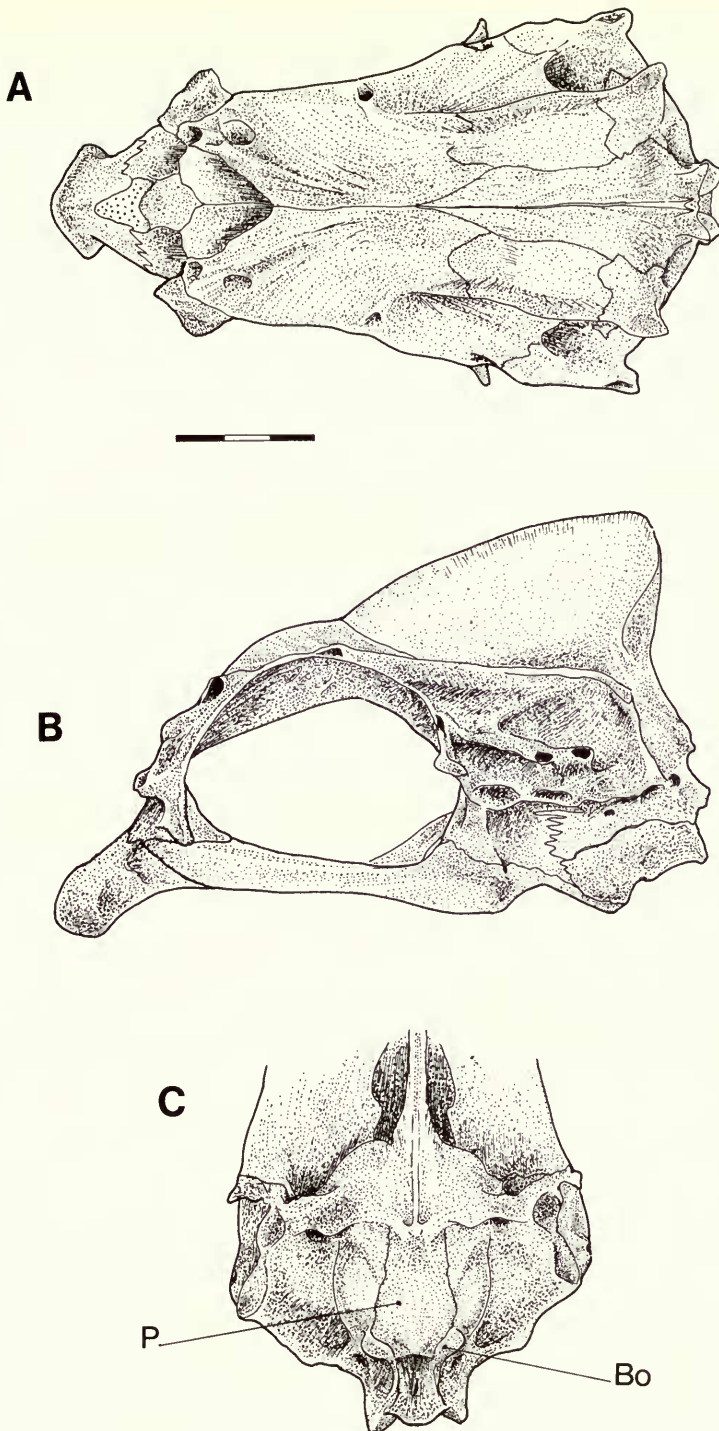


Fig. 22 Neurocranium of *Parananchromis longirostris* in A. Dorsal; B. Left lateral view. C. Neurocranial apophysis for the upper pharyngeal bones. Scale bar in mms. P = parasphenoid; Bo = basioccipital (BMNH 1903.7.28:77-83; one of the syntypes).

directed anteriorly (Fig. 4A). Anterior blade $3\frac{1}{2}$ –4 times in the overall length of the bone. No 'kukri'-shaped teeth on the lower pharyngeal bone (see p. 197).

Scales cycloid. Lateral-line with 27–30 scales; upper lateral-line separated at its highest point (*ca.* the 8th pored scale) from the dorsal fin base by $1\frac{1}{2}$ scales, and by one scale over the last 3–5 pored scales. Chest scales noticeably smaller than those on the belly and anteroventral aspects of the flanks, the size transition between these scales and those of the chest abrupt. The two or three median rows of scales on the chest are larger than those situated more laterally. There are 12 scales around the caudal peduncle.

Gill-rakers in the outer row of the first gill-arch of the typical group II pelmatochromine type (see p. 160). Microbranchiospines absent.

Vertebral column with 12–14 abdominal and 12–13 caudal elements (excluding the fused PU1 and U1 centra), giving a total count of 25 or 26. A well-developed supraneural (predorsal) bone present.

Caudal fin with slight sexual dimorphism in at least one species where the lower 3 or 4 rays in the upper lobe are produced; otherwise the caudal fin margin is slightly subtruncate to rounded in both sexes. Pelvic fins with the first ray produced in males, the second ray as long as or but slightly shorter than the first in females. Dorsal fin with 14–16 spines, anal with 3.

Apparently some sexual dimorphism in body coloration; at least one species (*P. caudifasciatus*) with a fairly extensive silvery sheen on the dorsal fin in sexually active females. No *Tilapia*-spot, or any markings resembling one, is developed.

In other features (as in many of those listed) *Parananochromis* resembles *Pelvicachromis*.

NOTES ON THE ANATOMY AND OTHER FEATURES. A shortage of material for deep dissections or for making osteological preparations has restricted the number of observations which can be made on the anatomy of *Parananochromis*; radiographs, however, are available for all three species.

The neurocranium in *P. longirostris* closely resembles that of *Pelvicachromis pulcher* (cf. Figs 22 & 19), except that the supraoccipital crest is, relatively, a little higher in the former species. The crest has a gently curved dorsal margin so that, as in *Pelvicachromis pulcher*, there is no obvious posterior peak; the anterior tip of the supraoccipital lies above the midpoint of the orbit. The length of the ethmovomerine region is contained about $3\frac{1}{2}$ times in the neurocranial length, and slopes at an angle of about 65° to the horizontal.

Unlike *Pelvicachromis pulcher*, the pharyngeal apophysis in all three *Parananochromis* species is of the typical *Haplochromis*-type, with clearly demarcated and moderately large basioccipital facets. Thys (1968a) makes no comments on the nature of this apophysis in either *P. longirostris* or *P. caudifasciatus*. Trewavas (1975:233), referring to *P. gabonicus*, notes that '... although the base of the skull was not examined in this unique specimen, the other characters indicate that it belongs to the group in which the apophysis ... is formed by the parasphenoid alone'. Presumably she was influenced, in making that remark, by her considering the species to be a *Nanochromis* (*sensu* Pellegrin), a genus which Regan (1922) placed in his division of cichlids having a *Tilapia*-type apophysis. I have examined the apophysis in Trewavas' specimen of *gabonicus*, and find that, in fact, it is of the typical *Haplochromis*-type. Stewart & Roberts (1984) were the first to record, but without further comment, that the apophysis in at least some true *Nanochromis* species is of the *Haplochromis*- and not the *Tilapia*-type. I have now been able to examine that apophysis in all described species of *Nanochromis*, and can confirm that in each it is of the *Haplochromis*-type.

The lateral commissure in *Parananochromis longirostris* is of the *Haplochromis*-type (Greenwood, 1986) and a precommissural bridge is present.

As far as can be told from radiographs, the shape of the neurocranium in *Parananochromis caudifasciatus* is like that of *P. longirostris*, but that of *P. gabonicus* has a lower supraoccipital crest, probably lower even than in species of *Pelvicachromis*.

The *infraorbital series* in all three species is complete (cf. that in *Nanochromis*; see p. 186), and the first infraorbital bone (lachrymal) has four openings to its laterosensory canal; in *P. longirostris*, the only species checked, about half of the second infraorbital overlaps the posteriorly directed flange of the lachrymal (Fig. 5C).

The *vertebral column* is composed of 25 or 26 vertebrae, comprising 12–14 abdominal and 12 or 13 caudal elements (the fused PU1 and U1 centra excluded). A single well-developed supraneural

(predorsal) bone is present (it is absent or greatly reduced in size amongst species of *Nanochromis*, see p. 187).

Gill-rakers on the cerato- and epibranchial of the first gill-arch are like those described for *Chromidotilapia* (see p. 160). There is, apparently, some interspecific variability in the extent to which the median membrane between the inner and outer rows of gill-rakers is developed. The membrane in *P. longirostris* is very low and barely produced into a tubercle between each pair of inner and outer rakers, whereas in *P. caudifasciatus* and *P. gabonicus* it is high, with prominent tubercles; in the latter species the tip of each outer-row raker on the ceratobranchial is noticeably produced and horn-like.

The *pharyngobranchial skeleton*, except for the pharyngeal bones, has been examined only in *P. longirostris*. In all three species the *lower pharyngeal bone* has a deep median indentation of its posterior margin and a short anterior blade (its length contained *ca.* $3\frac{1}{2}$ to 4 times in the overall length of the bone), features which impart a distinctly arrow-head outline to the bone. The lower pharyngeal teeth are somewhat widely spaced, few in number, and the outermost row is implanted very close to the margin of the bone.

The *upper pharyngeal bones* are subovoid in outline and, as in all other pelmatochromines (and the majority of African cichlids), are orientated so that their posteriorly directed margins form a broad and shallow V whose apex points anteriorly (see Fig. 4A).

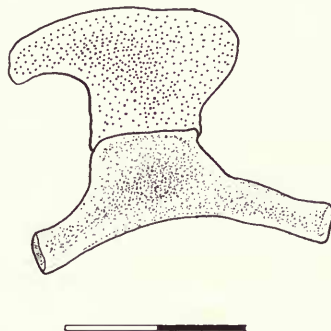


Fig. 23 Right epibranchial 2 of *Paranochromis longirostris* in dorsal view, to show the extensive cartilaginous flange (coarsely stippled) associated with its anterior border. Scale bar in mms. (BMNH 1903.7.28:77-83; one of the syntypes).

In *P. longirostris*, the only species dissected in depth, there is a very expansive, anvil-shaped cartilage developed on the anterior margin of the second epibranchial (Fig. 23); it almost fills the anterior part of the hanging pad, and extends to its anterior border.

Squamation. An unusual feature of *Paranochromis*, one which I would consider a possible synapomorphy for the lineage (but see p. 190), is the presence on the chest of 3 or 4 median rows of relatively but distinctly larger scales within the otherwise small scales of this area. The size transition between the small chest scales, and those on the ventrolateral aspects of the flanks and belly is abrupt.

Also characteristic of *Paranochromis*, but a feature shared with *Nanochromis*, is the reduced number (12) of circumpeduncular scales.

Cheek squamation patterns are interspecifically variable. In *P. gabonicus* there are two rows, with a deep naked strip ventral to the second row, and an extensive naked area anteroventrally; *P. caudifasciatus* has a large anteroventral naked area, but otherwise the cheek is covered by 3 or 4 rows of scales; *P. longirostris* has 2 or 3 scale rows, with a naked strip (about one scale row deep) along its entire ventral margin, and a large naked area anteroventrally.

The upper lateral-line is high on the body, with $1\frac{1}{2}$ scales separating it from the dorsal fin base at

its highest point (about the 8th or 9th pored scale), and one scale separating the fin base from the last 4 or 5 pored scales.

The scales on the nape and nuchal region are not noticeably reduced in size (cf. *Nanochromis*; p. 183).

Fins. Only an adult female of *P. gabonicus* is available, but in the other two species adult males have the first branched pelvic ray clearly longer than the second. In the female *P. gabonicus* the second ray is as long as the first, and in female *P. longirostris* and *P. caudifasciatus* the second ray is either as long as the first or is but marginally shorter, and consequently the apex of the fin is more nearly rounded than pointed.

The margin of the caudal fin is rounded to subtruncate in females of all three species, and, apparently, also in adult male *P. caudifasciatus*. Sexually active males of *P. longirostris*, however, have the margin of the upper caudal lobe, at about its mid-section, produced into a short, broadly triangular projection (see figure in Linke & Staeck, 1981:66). Judging from the figure of *P. gabonicus* in that publication (*op.cit.*:65), there is a slight indentation at about the mid-point of the posterior margin, but I have not been able to confirm this from preserved specimens.

Dentition. None of the three specimens has any particular character of note in its dentition, which is typically that of a group II pelmatochromine (see p. 158). Since only one small specimen is available (a 21 mm SL *P. caudifasciatus*) it is not possible to make any generalisations about possible ontogenetic changes in tooth form. In this small fish the outer teeth are unicuspid, but some teeth have faint traces of a shoulder below the major cusp; the crowns are but weakly curved, and no teeth with posteriorly directed crowns are present in the dentary. No inner row teeth are visible, even at a magnification of 30X.

Myology and arthrology of the jaws and gill-arches. Only *P. longirostris* has been dissected, and no outstanding features were noted in the musculature of the jaws.

In the dorsal pharyngobranchial musculature no part of the *levator posterior* muscle inserts on the horn of the lower pharyngeal bone. Except for a small tendinous slip inserting on the 4th epibranchial bone, all of the *levator externus* 4 muscle inserts on that horn. This condition is more like that in *Thysia* (see p. 163) than that in the other pelmatochromines. In those, a small part of the *levator posterior* inserts on the horn, and the insertion of the *levator externus* 4 on the epibranchial is musculose rather than tendinous.

In its ventral branchial musculature, *Parananochromis longirostris* is like the majority of pelmatochromines (and probably the other African cichlids; see Greenwood, 1985a:163) since a large part of the *obliquus ventralis* 3 muscle inserts on the semicircular ligament (*Pelvicachromis* is unusual in this respect, because in two of the three species dissected the muscle inserts entirely on the third hypobranchial bone; see p. 173).

Coloration. No information is available on the live colours of *P. gabonicus* (see Trewavas, 1975 for the preserved coloration of a female fish), and for *P. longirostris* the data are from a recently dead male (see Linke & Staeck, 1981:66). There is obvious sexual dimorphism in the coloration of *P. caudifasciatus* (see Linke & Staeck, 1981:58–59), although this may be less pronounced than in other pelmatochromines; these authors record a shiny, metallic band on the spinous dorsal fin of sexually active females (see p. 169).

Breeding biology. No information is available for either *P. gabonicus* or *P. longirostris*, but *P. caudifasciatus* is known to be a substrate spawner (Linke & Staeck, 1981:60).

Included species. At present only three named species can be referred to *Parananochromis*; that is *P. longirostris* (Blgr) 1903, *P. caudifasciatus* (Blgr) 1913 and *P. gabonicus* (Trewavas) 1975. Judging from Thys' (1968a) comments, however, more species will doubtless be added.

Two species, *Nanochromis robertsi* and *N. cavalliensis*, both described by Thys & Loisel (1971) have a close superficial resemblance to the species of *Parananochromis*, but on other and derived characters appear to belong to a lineage distinct from both *Nanochromis* and *Parananochromis* (see p. 188).

NANOCHROMIS Pellegrin, 1904.

TYPE SPECIES: *Pseudoplesiops nudiceps* Blgr, 1899 (by original designation).

SYNONYMY. *Pseudoplesiops* (*non* Bleeker): Boulenger, 1899 (the species *nudiceps* and *squamiceps*).

Nanochromis: Pellegrin, 1904, replacement name for *Pseudoplesiops* Blgr, 1899 (the species *nudiceps* and *dimidiatus*); Boulenger, 1915 (the species *nudiceps*, *dimidiatus* and *squamiceps*); Regan, 1922 (none listed); Stewart & Roberts, 1984 (the species *nudiceps*, *dimidiatus*, *squamiceps*, *transvestitus*, *consortius*, *parilius*, *minor* and *splendens*).

Pelmatochromis (*Nanochromis*), in part: Thys, 1968a (the species *nudiceps*, *dimidiatus* and *squamiceps*).

Since its original description (under the preoccupied name *Pseudoplesiops*) the genus has been defined and diagnosed principally on the high position of its upper lateral-line. In all but two species a little more than the posterior half of the upper lateral-line is contiguous with the base of the dorsal fin, and fewer than five scales anterior to the point of contiguity are separated from the fin base by more than one, or one and a half, often very small scales.

The exceptional species, *N. dimidiatus* and *N. squamiceps*, have only the last 3 to 5 scales of the upper lateral-line contiguous with the fin base, the greater part of the line having one very small scale interposed between it and the fin base. The supposed distinctness of these two species has been queried by Matthes (1964); however, in Thys' opinion (1968a:307) they are not only distinct but may not even be closely related.

The inclusion of *dimidiatus* and *squamiceps* in *Nanochromis* rather than in *Parananochromis* (see above, p. 176) is based on their having an interrupted infraorbital bone series in which only the lachrymal and one other canal bearing bone is present, the latter not curving around, and closing, the posterior margin of the orbit (see below).

Pellegrin (1904), when proposing the new name *Nanochromis* for the taxon (see synonymy), noted the presence of a clearly defined hanging pad in the pharynx, and was the first author to comment on the close similarity between *Nanochromis* and *Pelmatochromis* (then conceived in its broadest sense [see Introduction] but probably used by Pellegrin with particular regard to the species now placed in the genus *Pelvicachromis*). Regan (1922), too, commented on *Nanochromis* being 'Scarcely different from *Pelmatochromis*'. Neither author, however, gave any reasons for their views.

Thys (1968a:380) broadened the earlier concept of *Nanochromis* to include certain species here referred to the new genus *Parananochromis*, but reduced the status of *Nanochromis* to a subgenus of *Pelmatochromis*. His definition of *Pelmatochromis* (*Nanochromis*) was based, principally, on all its constituent species having a reduced number of scales (12) around the caudal peduncle since he expressed doubts about the significance of the high lateral-line position as a group character. In my view (p. 194) the high lateral-line is a good apomorphy indicating the monophyletic nature of the species possessing it, and also serves as one of the synapomorphic characters defining the taxon *Nanochromis*. The first really detailed taxonomic account of *Nanochromis* is Stewart & Roberts' (1984) paper, a follow-up of their earlier work describing a number of new species from the Zaire River (Roberts & Stewart, 1976). Although I would question some of the supposed autapomorphies used by Stewart & Roberts (1984) to establish the monophyly of *Nanochromis*, the other characters used by them appear to be good, and synapomorphic, features for that purpose (see discussion below).

That *Nanochromis* is a member of the group II pelmatochromine lineage is established by the nature of the dentition, the morphology of its gill-rakers, and by the well-developed, visor-like pharyngeal hanging pad.

Before presenting a diagnosis for *Nanochromis* some consideration must be given to the four supposed synapomorphic features which, in addition to the high upper lateral-line position, Stewart & Roberts (1984:82–83) used to establish the monophyly of the genus. These characters, and comments upon them, are:

(1) Only two infraorbital bones, a lachrymal with two lateralis canals extending to the lower rim and an elongate second infraorbital that projects posteriorly rather than follows the orbital rim; the infraorbital lateralis canal terminates posteriorly at a pore on the cheek.

Reduced and, or, variously interrupted infraorbital series occur in at least three other African cichlid taxa, viz. *Lamprologus* (*sensu lato*; see Colombe & Allgayer, 1985), *Telmatochromis* and *Julidochromis*. None of these, however, has the characteristic lachrymal plus one elongate, handle-like bone seen in *Nanochromis*, and all have various apomorphic features which are not shared with *Nanochromis*. Furthermore, none shares with *Nanochromis* the visor-like hanging pad and peculiar

dental features of a group II pelmatochromine (see p. 157), or the high-positioned upper lateral-line of that genus.

The nature of the infraorbital series in *Nanochromis* would therefore seem to be an autapomorphy. Stewart & Roberts' statement about the number of openings to the lachrymal latero-sensory canal could, at first sight, be misleading since there are four openings on that bone, the plesiomorphic condition in cichlids. Presumably the authors exclude from their count the anterior and posterior openings (which are shown in fig. 3 of Stewart & Roberts, 1984) since these could be interpreted as not reaching the bone's lower (i.e. ventral) rim.

The elongate second infraorbital in *N. squamiceps* and *N. dimidiatus*, unlike that in the other species, does follow the curvature of the eye, and thus does not project straight posteriorly in a handle-like fashion. However, as in the other species, the infraorbital bones in *N. squamiceps* and *N. dimidiatus* do not form a complete bony rim to the orbit, and the infraorbital canal (or at least its lower portion) terminates posteriorly as a pore on the cheek. Interestingly, both these species, as will become apparent below, tend not to show certain '*Nanochromis*' characteristics in the fully-developed manner seen in the remaining species.

(2) No predorsal bones.

The absence of predorsal bones (supraneurals) is a derived feature in cichlids, where one bone is the usual condition and two are found amongst African cichlids only in such plesiomorphic taxa as *Heterochromis* and *Tylochromis*; two predorsals are of more frequent occurrence in Neotropical genera (Cichocki, 1976:182; Oliver, 1984:29).

A single predorsal, usually small and comma-shaped, is visible in radiographs of *N. squamiceps*, *N. dimidiatus* and some *N. splendens* (the radiographed samples included some paratypes of all three species). It is absent, nevertheless, in all the examined material of the other *Nanochromis* species.

Clearly, there is an apomorphic trend within *Nanochromis* for the predorsal bone to be lost since even when present it is greatly reduced in size, and in at least one species (*N. splendens*) it is more often absent than present.

(3) Cheek and nape scaleless.

Reduced squamation, or its complete suppression in those particular areas of the body, occurs in other cichlids, and is usually associated with torrenticolous habits. But, as was the case with reduced infraorbital bones, the phenomenon in these other taxa is either linked with apomorphic features not shared by *Nanochromis*, or with the plesiomorphic condition of characters which are apomorphic in *Nanochromis*.

As Stewart & Roberts (1984) note, nape and cheek squamation is not greatly reduced in two species, *N. dimidiatus* and *N. squamiceps*, taxa which seem to constitute a plesiomorphic line within the genus. Thus, a scaleless nape and cheek, like the absence of a supraneural bone, could be interpreted as a synapomorphic condition uniting certain species within the genus, but not as one for the genus as a whole.

(4) Five lateralis pores on the mandible and seven on the preopercle, including one at its dorsal tip.

Such numbers for the openings in these canals are apparently universal amongst African cichlids. The character cannot therefore be considered a synapomorphy for *Nanochromis*.

In brief, of the four characters listed by Stewart & Roberts (1984), only the peculiarities exhibited in the infraorbital series can be considered an apomorphy for *Nanochromis* as a whole. It thus joins the extreme dorsal position of the upper lateral line as a defining synapomorphy for the genus.

DIAGNOSIS. *Nanochromis* is distinguished from all other African taxa by the following characters taken in combination: Body attenuated and slender, the dorsal head profile decurved or, if straight, sloping steeply (Fig. 24).

Neurocranial apophysis for the upper pharyngeal bones of the *Haplochromis*-type. Supraoccipital crest low, without a well-defined peak. Fronto-parietal crests weak. Supraethmoid not suturally united with the vomer.

Palatine with a two-point neurocranial contact, anteriorly through an articulation in the region of the ethmovomerine suture, and posteriorly with a facet on the ventral face of the lateral

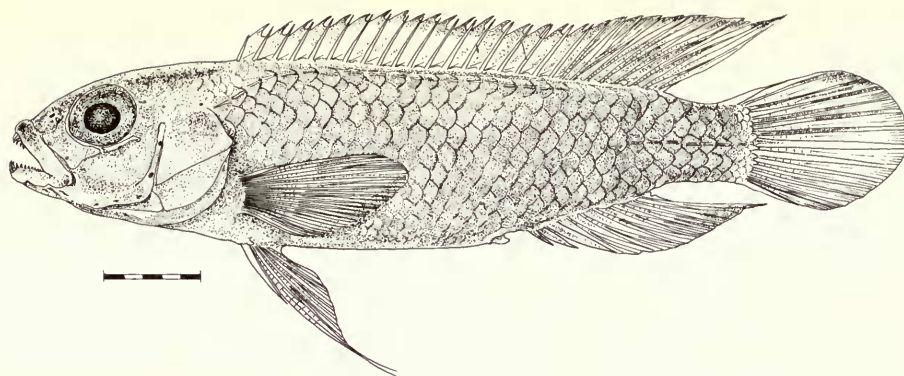


Fig. 24 *Nanochromis nudiceps*; one of the syntypes. Drawn by Gordon Howes. Scale bar in mms. (BMNH 1899.11.27:64).

ethmoid (see Greenwood, 1985a): A calyx is formed between the metapterygoid and the hyomandibula.

Infraorbital bone series reduced to the lachrymal and an elongate second bone closely articulated with the lachrymal from which it protrudes in a handle-like manner; there is a prominent pore in the cheek at the posterior end of the second infraorbital, coincident with the last lateralis pore in that bone. Lachrymal with four openings to its laterosensory canal system.

Lower jaw less than 50 percent of the head length. Ascending process of the premaxilla from slightly shorter to slightly longer than the alveolar arm. Anguloarticular with a roofed canal for the mandibulo-preopercular laterosensory canal.

Jaw teeth of the typical group II pelmatochromine type (see p. 158); the first appearance of posteriorly directed teeth situated anterolaterally in the lower jaw is correlated with the size of the fish (see p. 187).

A well-developed, clearly circumscribed, visor-like pad developed in the pharynx immediately anterior to the upper pharyngeal bones. Posterior facing margins of the major upper pharyngeal bones aligned so as to form a broad and shallow V, its apex directed anteriorly. Anterior blade of the lower pharyngeal bone relatively short, its length contained 3–4 times in the overall length of the bone. No 'kukri'-shaped teeth on that bone (see p. 197), the teeth of which all have the tip of the major cusp lying a little anterior to, or in the same vertical as the posterior margin of the tooth.

Scales cycloid, 23–28 in the lateral-line series. Cheek naked or partly scaled; nape and chest seemingly naked in most species (but very small, scattered and deeply embedded scales sometimes present), obviously scaled in others where the nape scales are neither noticeably small nor deeply embedded, but the chest scales are small and confined to the upper part of that region.

Upper lateral-line situated high on the body with, in most species, slightly more than its posterior half contiguous with the dorsal fin base, and with not more than one or one and a half scales between about the fifth pored scale in the series and the first pored scale which is contiguous with the dorsal fin base. Both lateral-line series in all species are often interrupted by the intercalation of several non-pored scales.

Twelve scales around the caudal peduncle.

Gill-rakers of the group II pelmatochromine type, but the tubercles are often small or difficult to detect, and the epibranchial rakers vary from short and broad to relatively slender; 6 to 9 rakers in the outer row of the first ceratobranchial, and 3–5 in a single row on the first epibranchial. Microbranchiospines are absent.

Total number of vertebrae 25–28, comprising 12–14 abdominal and 12–14 caudal elements (excluding the fused PU1 and U1 centra). Predorsal (supraneural) bone absent in five species, present or, more frequently, absent in another, and present but very small and comma-shaped in two others.

Caudal fin apparently showing no sexual dimorphism in the shape of its posterior margin. In all but one species the first pelvic ray in adult males is produced. In females the second ray is as long as or slightly longer than the first ray (a condition also seen in the adult males of *N. transvestitus*). Dorsal fin with 16–19 spines, anal with 3.

Marked sexual dimorphism in the coloration of adults (see p. 187). A dark mark resembling a *Tilapia*-spot occurs in at least two species.

Where breeding habits are known, the species are substrate guarders.

NOTES ON THE ANATOMY AND OTHER FEATURES. The small adult size attained by most *Nanochromis* species, combined with a paucity of material and its often indifferent state of preservation, has severely limited the amount of anatomical information which could be gained. Certain osteological data were obtained from radiographs of all described species, and certain soft anatomical features and osteological characters were studied from partial dissections of *N. nudiceps*, the type species, and *N. parilius* (one specimen of each).

The neurocranium of *N. nudiceps* (Fig. 25) has a very low supraoccipital crest whose dorsal margin slopes gently upwards at a low angle; the anterior point of the supraoccipital lies in a vertical passing through the middle of the orbit. Judging from radiographs, the situation is similar

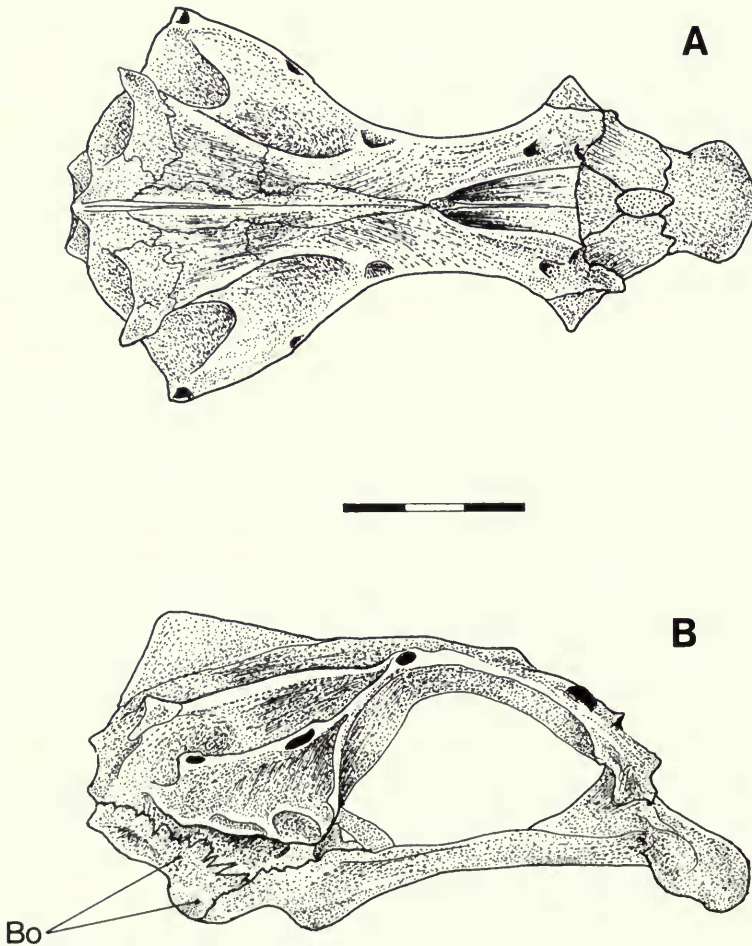


Fig. 25 Neurocranium of *Nanochromis nudiceps* in: A. Dorsal, and B. Right lateral view. Scale bar in mms. (Unregistered specimen; see text, p. 141). Bo = basioccipital.

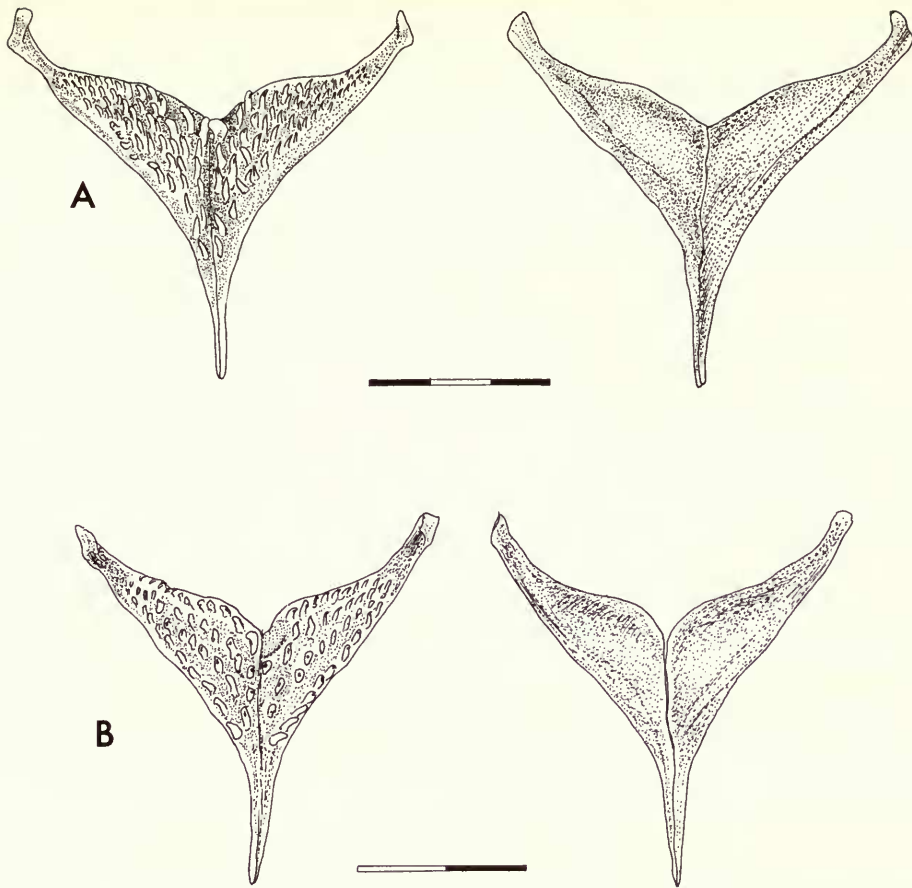


Fig. 26 Lower pharyngeal bones (dentigerous surface left, and ventral surface right) of: A. *Limbochromis robertsi*; holotype. B. *Nanochromis nudiceps* (unregistered specimen, see text, p. 141).

in all other species. The fronto-parietal crests are low and narrow. The ethmovomerine region, whose length is contained about $3\frac{1}{2}$ times in the neurocranial length, slopes at an angle of *ca.* 30° to the horizontal, its tip lying well below the level of the parasphenoid and the apophysis for the upper pharyngeal bone. That apophysis is of the *Haplochromis*-type, with substantial contributions by the basioccipital to its articular surface. The lateral commissure is broad and of the *Haplochromis*-type; no precommissural bridge is present (see Greenwood, 1986).

Apart from the low supraoccipital crest, the weaker fronto-parietal crests, and a narrower interorbital region, the neurocranium of *N. nudiceps* more closely resembles that in most *Pelvicachromis* species than it does the neurocranium in *Parananochromis longirostris* (see pp. 172 & 177 respectively).

What little information that could be obtained on other aspects of the cranial osteology (*jaws* and *suspensorium*) and of the *branchial skeleton*, suggests that no features depart significantly from those of other pelmatochromine taxa. However, it must be remembered that only one partial dissection was possible.

In all *Nanochromis* species the *lower pharyngeal bone* has a deep indentation in its posterior margin, and a short anterior blade which is contained *ca.* 3–4 times in the overall length of the bone, features which impart an arrowhead-like outline to the bone (Fig. 26B). Teeth on this bone are fine (except for the slightly larger teeth in the posterior transverse row, and those posteriorly in the median rows), are weakly cuspidate, and are fairly widely spaced.

The shape and orientation of the *upper pharyngeal bones* in all species are of the common cichlid type, with the near-ovoid upper pharyngeal bones of each side forming a deep and shallow V, its apex directed anteriorly. No other details are available for the pharyngobranchial skeleton.

The peculiar and particular arrangement of the two *infraorbital bones* present (the lachrymal and an elongate second bone) has been touched upon above (p. 181). In all species except *N. dimidiatus* and *N. squamiceps* the upper margin of the elongate second bone is virtually straight, and so does not conform closely to the posteroventral margin of the eye-ball. In outline, the lachrymal and the second bone resemble a simple drawing of a saucepan (Fig. 27).

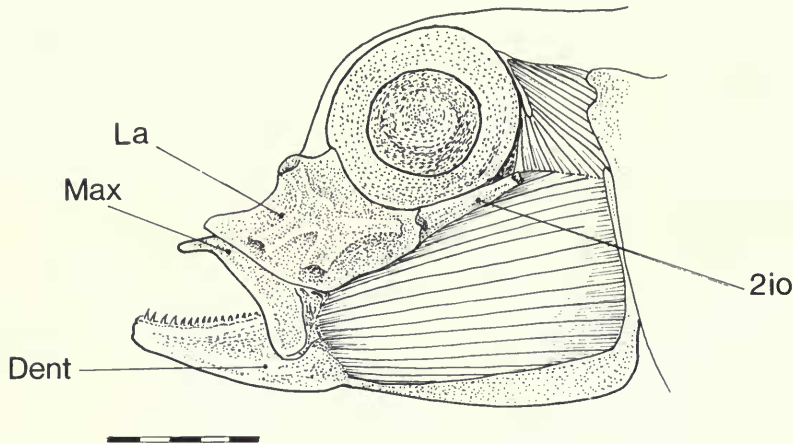


Fig. 27 The two infraorbital bones of *Nanochromis nudiceps* shown *in situ*. Scale bar in mms. (Same specimen as in Fig. 25). La = lachrymal; 2io = second infraorbital bone; Max = maxilla; d = dentary.

The two exceptional species have a second infraorbital whose upper margin is distinctly curved and so follows closely the eye's lower contours; the 'saucepan' outline is thus less obvious.

It has proved impossible to determine whether, ontogenetically, the second infraorbital is a single or a compound element. Some intraspecific variability exists in the number of laterosensory canal pores in this bone, with three being the usual condition but with only two pores sometimes present, either uni- or bilaterally. Four openings are invariable in the lachrymal.

The *squamation* in *Nanochromis* shows several unusual features. The high position of the upper lateral-line in all species, and the contiguity of somewhat more than its posterior half with the base of the dorsal fin in all but two of those, is one of the diagnostic apomorphies for the genus (see p. 183). Even in *N. squamiceps* and *N. dimidiatus*, the species with only the last 3–5 pored scales touching the dorsal fin base, more than the posterior two-thirds of the line is separated from the fin base by only a single scale.

Nanochromis squamiceps and *N. dimidiatus* also differ from their congeners in having the nape fully scaled (naked or with a few, small, scattered, and deeply embedded scales in the other species), and in the chest being partly scaled, but with the ventral and ventrolateral aspects naked. The chest is completely naked in all other *Nanochromis*.

In these species too, and unlike *N. squamiceps* and *N. dimidiatus*, the ventral face of the belly is naked from the pelvic fin insertions to the vent. The cheek in *N. squamiceps* is partially covered by three rows of scales, but there is an extensive naked area anteroventrally; this extends from the posteroventral margin of the lachrymal downwards to the preoperculum, and posteriorly almost to below the mid-point of the orbit. In the *N. dimidiatus* type specimens examined, the naked area is even larger, with only one or two scales present below the second infraorbital bone; these specimens, however, are now in a very poor condition so some scales could have been lost. The cheek is entirely naked in all other *Nanochromis* species.

Gill-rakers in *Nanochromis* are basically of the group II pelmatochromine type discussed on p. 159. There are 6–9 rakers in the outer row of the first ceratobranchial. Departure from the modal group II type of raker is manifest in the very small tubercles developed on the concave upper surface of the first ceratobranchial rakers; these may appear smooth when examined at a low magnification despite the large number of tubercles present.

Some, and apparently interspecific, variation occurs in the degree to which the median membrane between the inner and outer rows of rakers is developed on the first arch. But, as noted before, this could be a reflection of the specimens' state of preservation.

Only a single row of 3–5 epibranchial rakers is present on the first arch, and these vary interspecifically, from short and broad to slender and elongate.

As in other group II pelmatochromines, there are no microbranchiospines.

The *dentition* of *Nanochromis* shows no marked departure in tooth form or pattern from that of other group II pelmatochromines (see p. 158).

Because the size range of available specimens is so limited it has not proved possible to determine at what standard length the posteriorly orientated anterolateral dentary teeth first appear, or whether the definitive tooth form is preceded by one of a different kind (see pp. 144 & 158). In the sample of *N. transvestitus* examined, the smallest individual with posteriorly directed teeth in the dentary has a standard length of 24 mm, and the smallest *N. parilius* with such teeth is 31 mm SL.

The *vertebral column* is composed of 12–14 abdominal, and the same number of caudal elements (excluding the fused PU1 and U1 centra), giving total counts of 25–28.

In the single syntypical specimen of *N. squamiceps*, and the four syntypes of *N. dimidiatus* radiographed, a small, comma-shaped *predorsal bone* is present, as it is in two of the 10 *N. splendens* paratypes examined. In the specimens of all other species no trace of a predorsal bone is visible in the radiographs.

There apparently is no sexual dimorphism in the shape of the *caudal fin* margin, which is rounded in both sexes. The first branched *pelvic ray* of adult males is clearly the longest, although in some individuals the second ray can be almost as long as the first. Females have the second branched pelvic ray as long as, or slightly longer than the first, as is apparently the case in both sexes of *N. transvestitus*. (For a discussion of this character, see p. 169).

There are 16–19 spinous rays in the *dorsal fin* and 3 in the *anal*.

The little information gained from a partial dissection of a *N. nudiceps* specimen showed no outstanding features in the *myology and arthrology* of the jaws. No data are available for the *pharyngeal and branchial musculature*.

Coloration. All species of *Nanochromis* have a marked sexual dimorphism in adult coloration (see Roberts & Stewart, 1976, and especially the colour photographs in Linke & Staeck, 1981); one species, *N. transvestitus* is very unusual amongst African cichlids in having the female more brightly coloured than the male (Stewart & Roberts, 1984).

At least two species, *N. splendens* and *N. dimidiatus*, seem to have a *Tilapia*-spot on the soft dorsal fin of some individuals (Roberts & Stewart, 1976:29; and Linke & Staeck, 1981: 63, for the species respectively). *Nanochromis dimidiatus* females, when adult, are also interesting in that a silver blotch is developed on the flank above the genital opening. A similar silver mark is otherwise known only in *Thysia* (see Loiselles & Welcomme, 1972; colour photograph in Linke & Staeck, 1981:135), and in specimens identified by Voss (1980:23, 25 & 27) as *Pelvicachromis subocellatus*. Such a mark has not been recorded, as far as I am aware, in other African cichlids.

Breeding biology. All species of *Nanochromis* are substrate guarders; for detailed accounts of spawning habits see Linke & Staeck (1981).

Included species: *Nanochromis nudiceps* (Blgr) 1899; *N. consortius* Roberts & Stewart, 1976; *N. dimidiatus* (Pell.) 1904; *N. minor* Roberts & Stewart, 1976; *N. parilius* Roberts & Stewart, 1976; *N. splendens* Roberts & Stewart, 1976; *N. squamiceps* (Blgr) 1902; *N. transvestitus* Stewart & Roberts, 1984.

Intrageneric relationships

If it be accepted that the interrupted and reduced series of infraorbital bones (see p. 181 above), and the high-set upper lateral-line with at least the last 3–5 pored scales contacting the dorsal fin base,

are unifying synapomorphies for *Nanochromis*, then two groups of species can be recognised within the genus.

The smaller group, comprising the species *N. squamiceps* and *N. dimidiatus* is characterised by having only the last 3–5 pored scales of the upper lateral-line contiguous with the dorsal fin base, a completely scaled belly and nape, a partially scaled chest and cheek, and by the presence of a predorsal bone (albeit reduced and comma-shaped) in all individuals.

The second and larger group, contains all the remaining species. It is characterised by having the posterior half (or slightly more) of the upper lateral-line contiguous with the dorsal fin base, a naked nape, cheek and belly, and by the absence of a predorsal bone (at least in the majority of individuals, see p. 187 above). In all these features members of the group exhibit a more derived state than is shown by either *N. squamiceps* or *N. dimidiatus*.

For the moment it would seem preferable to treat the two groups informally and not recognise them as subgenera. That decision, however, may well be revised when more is known about the soft anatomy, the osteology and the breeding habits of all *Nanochromis* species.

LIMBOCHROMIS gen. nov.

TYPE SPECIES: *Nanochromis robertsi* Thys van den Audenaerde & Loisélle, 1971.

SYNONYMY. *Nanochromis* (non Pellegrin, 1904): Thys & Loisélle, 1971 (the species *robertsi* and *cavalliensis*).

ETYMOLOGY. From the Latin *limbus*, an edge, and *chromis*; *limbus* in this particular context is used more in the spirit of its common English form of 'in limbo'.

This new genus represents a taxonomic defeat. It is established for two species which, although clearly members of the group II pelmatochromine assemblage, cannot be included in any of the genera recognised here, nor can it be identified as a sister group to any of those taxa.

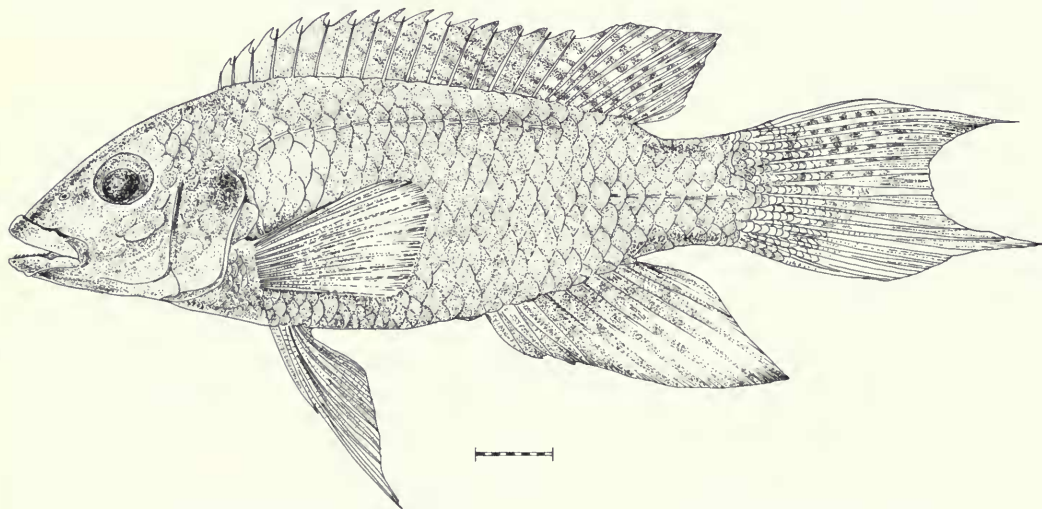


Fig. 28 *Limbochromis robertsi*; holotype (SU 63143). Scale bar in mms. Drawn by Gordon Howes.

Thys & Loisélle (1971:20), with obvious misgivings, referred their two new species to *Nanochromis* (*sensu* Thys, 1968*a*) simply because both have a reduced number of circumpeduncular scales, namely 12–14. The authors noted that both species differed from the concept of *Nanochromis* which they were using in having the caudal fin margin produced into a pair of streamer-like points, and that the geographical distribution of both species lay outside the range of other species referred to that genus (then treated as a subgenus) by Thys (1968*a*).

As *Nanochromis* is now restricted to species having part of the lateral-line contiguous with the dorsal fin base, only two infraorbital bones, and a *Haplochromis*-type of neurocranial apophysis for the upper pharyngeal bones (see pp. 182–184), neither *robertsi* nor *cavalliensis* can be considered members of that genus. In both species the upper lateral-line is completely separated from the dorsal fin base (by at least one scale at its nearest point of approach to the fin), the infraorbital series is complete, and the neurocranial apophysis is of the plesiomorphic *Tilapia*-type. Furthermore, neither species has, in either sex, the length of the second branched pelvic ray equal to, or slightly longer than the first ray.

The pelvic fins and the plesiomorphic condition of the neurocranial apophysis in *robertsi* and *cavalliensis* serve to exclude the species from membership of the genus *Parananochromis*, a taxon which, in their general habitus, they resemble more than they do any species of *Nanochromis*.

Again, the nature of the pelvic fins excludes *robertsi* and *cavalliensis* from *Pelvicachromis* (see p. 169), as does the reduced number of circumpeduncular scales (12 or 13 in *cavalliensis*, 14 in *robertsi*, compared with 16 in all *Pelvicachromis* species). The plesiomorphic pharyngeal apophysis in both *Pelvicachromis* and the two species under review, is, of course, valueless for establishing any possible relationship between them.

It is for these various reasons that I have erected the genus *Limbochromis* for the species *robertsi* and *cavalliensis*. Its monophyly would seem to be attested by a reduced number of scales around the caudal peduncle occurring in species which do not share, with other pelmatochromines having that feature, the derived *Haplochromis*-type pharyngeal apophysis on the skull or an elongate second pelvic fin ray in females.

The question then arises as to whether or not the reduced peduncular scale count in *Limbochromis* indicates its relationship, as the plesiomorphic sister group, to *Parananochromis* and *Nanochromis* combined. Here one is faced with a dilemma which I do not think can be settled until more information is available about the four taxa which must be involved in solving that problem, viz. *Limbochromis*, *Pelvicachromis*, *Parananochromis* and *Nanochromis*.

The three latter taxa share one apparently synapomorphic feature, namely, pelvic fins in females which have the second branched ray longer than the first. *Parananochromis* and *Nanochromis*, however, have the derived *Haplochromis*-type pharyngeal apophysis but *Pelvicachromis* has the plesiomorph *Tilapia*-type; the two former species have a reduced (i.e. derived) number of scales around the caudal peduncle but *Pelvicachromis* does not.

Thus, using their one synapomorphic feature (pelvic fins), *Pelvicachromis* could be interpreted as the plesiomorphic sister taxon of *Parananochromis* and *Nanochromis*. If that argument is accepted, then the reduced circumpeduncular scale count, the only derived character shared by *Limbochromis* and the *Nanochromis*-*Parananochromis* generic pair, is not a synapomorphy but a homoplastic feature.

As a counter argument one could propose that the reduced scale count is the true synapomorphy (shared by *Limbochromis* and the *Nanochromis*-*Parananochromis* pair) and that the pelvic fin feature is the homoplastic one independently derived in *Pelvicachromis*. In this case, *Limbochromis*, would be the plesiomorphic sister taxon of the *Nanochromis*-*Parananochromis* generic pair.

In the absence of other and differentially congruent synapomorphic features which might refute one or other of those arguments, either solution would seem equally parsimonious (see also p. 194).

DIAGNOSIS. Since so little material of either species is available for study, the diagnosis is, perforce, based essentially on superficial characters. *Limbochromis* (Fig. 28) closely resembles *Parananochromis* except that:

- (1) The neurocranial apophysis for the upper pharyngeal bones is of the *Tilapia*-type, i.e. formed entirely from the parasphenoid.
- (2) There are 12–14 (modally 12 or 13) scales around the caudal peduncle.
- (3) The first branched pelvic fin ray in adult females is clearly longer than the second ray; dorsal fin with 15 or 16 spines.
- (4) Bilateral naked patches are present on the chest in one species.
- (5) The upper lateral-line at its highest point (the 8th pored scale) is separated from the dorsal fin

base by two large and one very small scale, or by $1\frac{1}{2}$ scales; posteriorly, the last 3 or 4 pored scales are separated from the fin base by $1\frac{1}{2}$ scales, or by one large and one very small scale; lateral-line with 28 or 29 scales; chest scales moderately small, with a fairly abrupt size transition between them and those on the ventrolateral aspects of the flanks and belly.

(6) Vertebral column with 26 vertebrae (excluding the fused PU1 and U1 centra) comprising 13 or 14 abdominal and 12 or 13 caudal elements.

(7) Caudal fin in adult males of one species (*L. robertsi*) with two, symmetrically produced streamers; probably with two shorter projections in females. Nature of caudal fin margin in adult males unknown for the second species (*L. cavalliensis*), but adult females have a short projection; caudal margin subtruncate to rounded in young.

(8) No data available on live colours in *L. cavalliensis*, but there is pronounced sexual dimorphism in *L. robertsi* (see Linke & Staeck, 1981: 74–75).

NOTES ON THE ANATOMY AND CERTAIN OTHER FEATURES. Because no deep dissections could be made on the few available specimens, and since no osteological preparations exist, virtually nothing can be said about the musculature and the skeleton of *Limbochromis*. Those characters which could be investigated by superficial dissection, and from radiographs, do not depart greatly from the usual pelmatochromine group II condition or, indeed, from that of the pelmatochromines as a whole.

The *dentition and gill-rakers* are typically those of group II pelmatochromines, as is the absence of microbranchiospines (see p. 157). Nothing is known about size-correlated changes in tooth form, or at what size the posteriorly directed anterolateral teeth in the dentary first appear.

The shape of the *lower pharyngeal bone* (Fig. 26A) and the nature of the *lower pharyngeal teeth* show no outstanding features, and the shape, dentition and orientation (a broad, shallow V) of the *upper pharyngeal bones* are like those in other group II pelmatochromine species.

One unusual feature, with respect to most other pelmatochromines, is the occurrence, in one species, of five rather than four openings to the *lachrymal laterosensory canal* system. The occasional occurrence of five openings in *Pelvicachromis* has been reported (but not confirmed) by Trewavas (1983) and five openings are usual in all but one species of *Chromidotilapia* (see p. 168).

It is obvious that some sort of sexual dimorphism occurs in the shape of the *caudal fin* margin (see Thys & Loiselle, 1971), but its exact nature is still undetermined. The seemingly symmetrical development of streamer-like prolongations from both the upper and lower lobes of the caudal fin's posterior margin in one species (*L. robertsi*; see Fig. 28) is unusual amongst African cichlids, but seems to be repeated, albeit weakly, in the other species of *Limbochromis*. More information is needed about this feature, as are detailed accounts of live colours in sexually active fishes.

Judging from the radiographs, *neurocranial shape* in *Limbochromis* is like that in *Parananochromis*. A well-developed, dagger-like *predorsal (supraneural) bone* is present. The *vertebral column* has 13 or 14 (mode) abdominal, and 12 (mode) or 13 caudal centra (excluding the fused PU1 and U1 centra), with a total count of 26.

As in some other group II pelmatochromines, the upper *lateral-line* in *Limbochromis* has a relatively high position on the body, with its highest point (the 8th pored scale) separated from the dorsal fin base by $1\frac{1}{2}$ to 2 large and one very small scale; posteriorly, the last 3 or 4 pored scales are separated from the fin base by $1\frac{1}{2}$ scales or one large and one very small scale. The cheek is partly covered by 3 or 4 rows of scales, with a large naked area anteroventrally, and in one species, a narrow, naked strip below the scaled area. Chest scales are small, and have a relatively abrupt size transition with those on the ventrolateral aspects of the flanks. In *L. robertsi*, but not in *L. cavalliensis*, the scales on the medioventral aspect of the chest are somewhat larger than those occurring laterally (i.e. as in *Parananochromis*, see p. 179); *L. cavalliensis*, but not *L. robertsi*, has a small and bilateral naked patch on the anterolateral aspect of the chest.

What information there is on the *breeding biology* of the two *Limbochromis* species (see Thys & Loiselle, 1971: 198, 199, and 202–203), does not indicate that either is a mouth-brooder.

Included species. *Limbochromis robertsi* (Thys & Loiselle) 1971, and *Limbochromis cavalliensis* (Thys & Loiselle) 1971.

The phylogenetic relationships of the pelmatochromine taxa

One of the objects of this paper is to investigate whether the pelmatochromine fishes of Thys (1968*a*, see p. 139) are a distinct and monophyletic lineage within the African Cichlidae, and if that is so, what is their relationship to other African lineages.

For the moment, Thys' (1968*b*) transfer of his subgenus *Pelmatochromis* (*Pelmatochromis*) to *Tilapia* will be ignored; his action was challenged and rejected by Trewavas (1973), and my reasons for rejecting it will be discussed later (p. 195). Thus the pelmatochromine genera concerned are those originally defined by Thys (1968*a*) as subgenera of *Pelmatochromis*, and subsequently modified by Loiselle & Welcomme (1972), Trewavas (1973 & 1974) and in this paper.

The genera involved are: *Pelmatochromis* Steindachner, *Thysia* Loiselle & Welcomme, *Chromidotilapia* Blgr, *Pelvicachromis* Thys, *Parananochromis* gen. nov., *Nanochromis* Pellegrin, and *Limbochromis* gen. nov.

For the purposes of this discussion, a monophyletic lineage is recognised by all its constituent taxa uniquely sharing one or more derived characters which would suggest their having stemmed from a recent common ancestor with that or those features. Thus, although all pelmatochromines have at least two supposedly derived features, cycloid scales and unicuspid oral teeth when adult (see p. 143), these are shared with a large number of other taxa: I would interpret that level of synapomorphy as possibly indicative of a remote rather than a recent shared ancestry, if it is not an example of homoplasy.

As indicators of recent common ancestry I have chosen those synapomorphic features which are shared by fewer species, using the extent of their occurrence amongst different taxa to build up various hierarchical levels of relationship. For example, a well-developed, visor-like hanging pad developed from the pharyngeal roof (p. 157) is a derived feature shared by several pelmatochromines, and is congruent with four other apomorphic features (see pp. 157–160). In brief, they involve the absence of microbranchiospines, the morphology of the oral teeth, and the morphology of the gill-rakers on the first gill-arch. The apomorphic status of all these characters is based on outgroup comparisons within the family, the suborder Labroidei and other percoid fishes as well.

A sixth character may also indicate a common ancestry for this group, but it occurs mosaically and its derived status has still to be ascertained with certainty. This feature is the presence of a well-defined silver spot or blotch situated immediately above the ano-genital region of sexually active female fishes. It has been recorded in *Thysia*, one *Pelvicachromis* species, and in *Nanochromis dimidiatus* (see respective generic descriptions for references). Unfortunately, live colours are known for relatively few cichlids, thus making it impossible to determine, with reasonable certainty, whether this seemingly derived characteristic is indeed an apomorphy.

The five principal synapomorphies noted above occur together in *Thysia*, *Chromidotilapia*, *Pelvicachromis*, *Parananochromis*, *Nanochromis* and *Limbochromis*, and are taken to indicate the monophyletic status of that assemblage, the individual genera of which are themselves defined on the basis of each having one or more of its own autapomorphic characters.

The two remaining pelmatochromines, *Pelmatochromis* and the monotypic *Pterochromis*, share none of the five features discussed above; the relationship of *Pterochromis* can be dealt with rapidly, but regrettably, rather unsatisfactorily.

Pterochromis shares no derived features with either *Pelmatochromis* or, as noted above, with the *Thysia-Limbochromis* complex, except of course for those suggesting relationship at a much more inclusive level than we are concerned with here.

The unicuspid teeth of *Pterochromis*, relatively stout and with conical crowns, are of a generalized type amongst unicuspid, and are quite unlike those in the *Thysia-Limbochromis* group. Its long, slender and fine gill-rakers on the first arch are a derived feature, but are unique amongst the taxa under discussion (including *Pelmatochromis*). Similar rakers do occur within the tilapiine cichlids (*sensu* Trewavas, 1983) but *Pterochromis* does not share a single derived feature with any tilapiine taxon. The gill-rakers, therefore can be considered an autapomorphic feature for *Pterochromis*.

Likewise, the elongate lower jaw, long premaxillary ascending processes, and the steeply inclined

mouth of *Pterochromis* must be considered autapomorphies since none is congruent with other derived features occurring in taxa sharing those particular oral specialisations.

Thys (1968a) and Trewavas (1973) suggest that *Pterochromis* is a specialised form derived from *Pelmatochromis ocellifer*, but neither author discussed that idea in any detail; the proposed relationship would seem to be based on the shared plesiomorphic characters of the two taxa. Certainly no unique synapomorphies are shared by them, thus making it impossible to establish such a phylogenetic history.

The inadequate study material of *Pterochromis* has severely restricted investigations of its anatomy and osteology, and almost nothing is known about the biology of the species. Thus, for the moment, and based only on the superficial features discussed here and on page 155, I can suggest no testable hypothesis of relationship for the genus, and would exclude it from even an informal association with the other pelmatochromine taxa.

Pelmatochromis provides a rather different sort of problem. Like *Pterochromis* it shows few derived features, has well-developed microbranchiospines, and lacks a visor-like pharyngeal hanging pad, thus excluding it from actual membership of the *Thysia-Limbochromis* group (see p. 157).

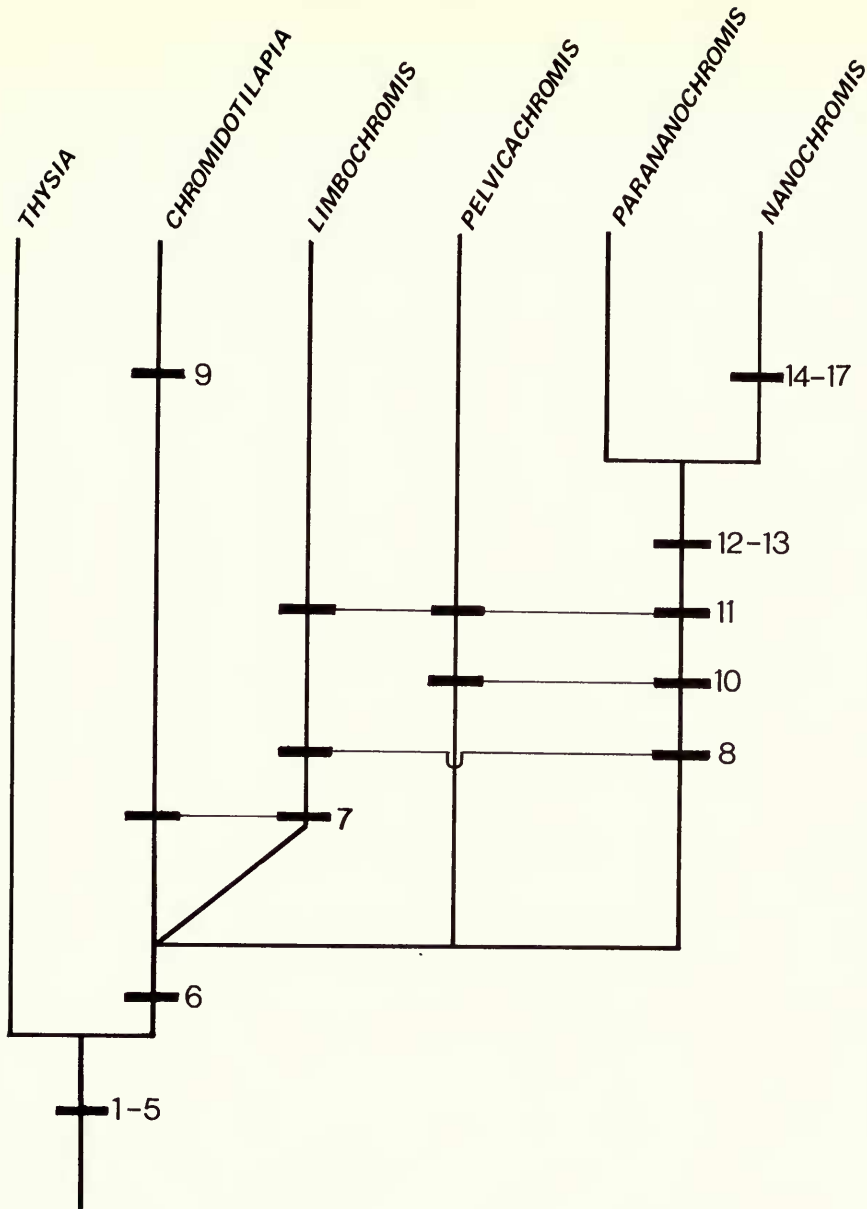
Indeed, there seems to be not a single unequivocal autapomorphy on which to define the genus (see p. 146). Its status as a discrete taxonomic entity is therefore based simply on its having a suite of characters, both apo- and plesiomorphic which, taken in combination, distinguish it from other and superficially similar taxa.

Pelmatochromis, like *Pterochromis*, has unicuspid outer row jaw teeth, and as in the latter genus, their cusp form is of a simple conical type, differing from the compressed-conical cusps in members of the *Thysia-Limbochromis* group (see p. 157); also, unlike members of that group, *Pelmatochromis* has no posteriorly directed teeth situated anterolaterally in the lower jaw.

The outer row gill-rakers on the first ceratobranchial of *Pelmatochromis* species are very unlike those in *Pterochromis* and, indeed, those in the majority of African cichlids. Their closest morphological counterparts are to be found in members of the *Thysia-Limbochromis* lineage. They could, in fact, be described as somewhat simplified versions of the rakers in that lineage (see p. 146).

Gill-rakers, then, are the sole derived features in *Pelmatochromis* which might indicate its relationship. With only that character available I would, at best, suggest an informal and very tentative status for *Pelmatochromis* as the putative and plesiomorphic sister group of the *Thysia-Limbochromis* lineage. Certainly, and unlike *Pterochromis*, there are no apomorphic features

Fig. 29 Diagram showing the distribution of various derived features amongst the chromidotilapiine cichlids (see pages 194–195); this figure can be used as a key to the genera. (1) Visor-like hanging pad in the pharynx (p. 157). (2) Outer teeth in both jaws unicuspid, with the labial surface of the crown flattened and the lingual aspect convex, resulting in the crown having well-defined and acute margins (p. 158 & Fig. 8). (3) A few teeth situated anterolaterally in the lower jaw so orientated that the crowns point posteriorly and not buccally (Fig. 9). (4) No microbranchiospines. (5) Ceratobranchial gill-rakers in the outer row of the first gill-arch pachydermatous, transversely aligned, with a tuberculate and concave upper surface and a protracted distal tip (p. 159 & Fig. 11). (6) Two large scales and one very small scale, or fewer scales ($1\frac{1}{2}$ the modal number) between the dorsal fin base and the highest point of the upper lateral line (the 8th or 9th pored scale). (7) Five openings to the laterosensory canal system in the lachrymal (1st infraorbital) bone (but one species in each genus with only four openings). (8) 12–14 scales around the caudal peduncle. (9) Mouth brooders. (10) The 2nd (sometimes the 2nd and 3rd) branched pelvic fin ray of females longer than the 1st branched ray, giving the distal tip of the fin a rounded rather than a pointed appearance. (11) Small to very small scales on the chest (which is entirely naked in some species, and has naked areas in a few others). (12) Neurocranial apophysis for the upper pharyngeal bones formed by the parasphenoid and basioccipital bones (i.e. of the *Haplochromis*-type), see p. 178. (13) Twelve scales around the caudal peduncle. (14) Only two bones in the infraorbital series (the lachrymal and one other bone articulating with it; see p. 186). (15) At least the last 3 or 4 pored scales of the upper lateral line contiguous with the fin base in most species. (16) Predorsal (supraneural) bone absent in many species, small and reduced in the others; see p. 187. (17) Supraoccipital crest low.



shown by *Pelmatochromis* which would preclude its representing a morphotype from which the less derived members of the *Thysia-Limbochromis* line could have evolved.

In brief, out of the original, if somewhat informally recognised pelmatochromine group of Thys (1968a), one monophyletic assemblage can be recognised on the basis of various synapomorphies. It comprises the genera *Thysia*, *Chromidotilapia*, *Pelvicachromis*, *Limbochromis*, *Parananchromis* and *Nanchromis*. As an informal epithet for that lineage, I propose the term 'chromidotilapiines'.

The two remaining genera, *Pterochromis* and *Pelmatochromis* are currently of indeterminable phyletic affinity, although there is some suggestion that *Pelmatochromis* might be the sister group of the chromidotilapiines (see above).

The intrarelationships of the chromidotilapiines

A tentative intragroup phylogeny for the chromidotilapiines is set out in Fig. 29.

The first dichotomy is based on the number of scales between the highest pored scale in the upper lateral-line (usually the 8th or 9th) and the base of the dorsal fin. *Thysia*, having the highest count ($2\frac{1}{2}$ or 3 scales) and sharing no other derived features with the other species, except the group synapomorphies discussed earlier, is taken to be the plesiomorphic sister taxon to all the others combined.

The derived characteristic of these other taxa lies in their having the dorsal fin base separated from the high-point of the lateral-line by no more than two large and one very small scale, or, as is modal for the group, one and a half or one scale.

The first division of this group is in the form of an unresolved polychotomy caused by *Limbochromis* (see discussion on p. 189). That genus shares some derived features with the more apomorphic members, but its apomorphies are combined with certain plesiomorphic features which are represented apomorphically in the other taxa. *Pelvicachromis* occupies, as it were a 'mirror-image' position with respect to the same characters.

In addition to the possible relationships discussed on p. 189, a fully resolved cladogram could be produced if two other assumptions were made. First, that the apparent plesiomorphy of the high circumpeduncular scale count in *Pelvicachromis* actually represented a secondary, that is derived, return to the plesiomorphic condition from the low counts in *Limbochromis*, *Parananochromis* and *Nanochromis*. Second, that the derived number of laterosensory pores (5 cf. 4) in certain *Chromidotilapia* and *Limbochromis* species represents a homoplastic rather than a synapomorphic feature. Such a cladogram, based on those assumptions and employing the other characters used in Figure 29, would make *Limbochromis* the plesiomorphic sister group of *Pelvicachromis*, *Parananochromis* and *Nanochromis* combined, and *Pelvicachromis* the plesiomorphic sister taxon of *Parananochromis* and *Nanochromis*.

However, since the two assumptions are untestable at present, this solution is no more satisfactory than that discussed before (p. 189). Thus, for the moment, a polychotomous arrangement would seem to be the only acceptable one.

Within the polychotomy, *Chromidotilapia* and *Limbochromis* have retained the plesiomorphic condition of the pelvic fin in females, with the first branched ray longer than the second, as it is in males also. *Chromidotilapia* has slightly more scales (2 plus one very small scale) above the high-point of the lateral-line and the dorsal fin base than does one species of *Limbochromis* (the other has the same number as *Chromidotilapia*). *Chromidotilapia* also retains the plesiomorphic feature of large chest scales (small, sometimes with naked areas in the other taxa). No data are available on the breeding habits of *Limbochromis*, but *Chromidotilapia*, uniquely amongst the chromidotilapiines, is a mouth brooder. Another derived feature in that genus is the presence of five laterosensory canal openings in the lachrymal (but one species retains the plesiomorphic number of four); however, one of the two *Limbochromis* species also has five openings. Both *Limbochromis* species show the derived condition of a reduced scale count around the caudal peduncle, a feature not shared with either *Pelvicachromis* or *Chromidotilapia*, but one shared with two members of the fourth branch to the polychotomy, namely *Nanochromis* and *Parananochromis*. Both *Chromidotilapia* and *Limbochromis*, like *Pelvicachromis*, have the plesiomorphic *Tilapia*-type pharyngeal apophysis on the skull base.

Pelvicachromis together with the *Parananochromis*-*Nanochromis* generic pair, are characterised by having the derived pelvic fin condition where, in females, the second or second and third branched rays are longer than the first ray. Other synapomorphies shared by the three taxa (and approached by *Limbochromis*) are their small to very small chest scales abruptly size-demarcated from the scales on the ventrolateral aspects of the flanks, and a further reduction in the number of scales ($1\frac{1}{2}$, rarely 2) between the high-point of the upper lateral-line and the dorsal fin base; again a characteristic found in one *Limbochromis* species.

A major dichotomy in this assemblage is that between *Pelvicachromis* with its plesiomorphic *Tilapia*-type pharyngeal apophysis, and *Parananochromis* and *Nanochromis* which have the

derived *Haplochromis*-type. Both the latter genera are further linked by sharing a reduced number of scales around the caudal peduncle, 12 as compared with 16 in *Pelvicachromis*.

The dichotomy between *Parananochromis* and *Nanochromis* is based on three autapomorphic features of the latter taxon, viz. only two bones in the infraorbital series (see p. 186), at least the posterior quarter and usually the posterior half of the upper lateral-line contiguous with the dorsal fin base, and the predorsal bone either absent or, in a few species, very greatly reduced in size. Furthermore, in all but two *Nanochromis* species the scales on the chest are also greatly reduced in size, often with large naked areas, and in some species are completely absent (see p. 186).

In most respects this hypothesis of relationships within the chromidotilapiines is both inadequate and unsatisfactory. It can only be considered as a target for further attempts based on more detailed anatomical studies and the use of other and non-morphological characteristics.

From an evolutionary point of view the various chromidotilapiine genera, from *Thysia* at one extreme to *Nanochromis* at the other, show a clear cut reductional trend in a number of characters. These involve the overall body shape (from deep and barely compressed to slender and elongate), a decrease in the number of scales between the lateral-line and the dorsal fin base, a reduction in the number of scales around the caudal peduncle, and a reduction in the size of the scales on the chest (leading to partial or complete suppression in some taxa).

The contrast between the end-points of these trends, as represented by *Thysia* and *Nanochromis*, is very marked, yet within the assemblage the trend is certainly a very gradual one with the various stages represented by species of different genera. That phenomenon provides an interesting parallel with a similar pattern of change, but one involving different characters, amongst the endemic haplochromine species of Lake Victoria, and for which the term cladistic gradualism was coined (Greenwood, 1981; 1984b).

Intrafamilial relationships of the chromidotilapiines, *Pelmatochromis* and *Pterochromis*

The phyletic integrity of the chromidotilapiines seems well-established on the basis of various synapomorphic characters (see above). Two of those characters, the absence of microbranchiospines and the presence of a visor-like hanging pad in the pharynx, occur in other African cichlids. The phyletic significance of that fact cannot be properly evaluated in the present state of our knowledge about suprageneric affinities in the Cichlidae. What information we do possess certainly does not suggest a recent common ancestry for the taxa having those features. Rather it would suggest their repeated evolution in different lineages (see Greenwood, 1983).

Earlier suggestions that, through *Thysia*, the chromidotilapiines could be related to the *Hemichromis*-*Anomalochromis* lineage (see Loiselle & Welcomme, 1972) cannot be substantiated on the basis of uniquely shared apomorphies (see Greenwood, 1985a & b). The *Hemichromis*-*Anomalochromis* group is another of those cichlid lineages easily defined on the basis of its autapomorphic characters, but otherwise only showing a suite of widely occurring and plesiomorphic features which give no indication of its nearest relatives.

Outside the chromidotilapiines, *Pelmatochromis* provides a particularly intriguing phylogenetic puzzle. Although its supposed close relationship to the chromidotilapiines (Thys, 1968a) cannot be satisfactorily substantiated (see p. 192), its generalised oral dentition and the derived form of its gill-rakers would seem to favour the possibility of it being the plesiomorph sister taxon to that lineage (see above, p. 193).

In complete contrast to that possible relationship is the other suggestion put forward by Thys (1968a & b), that *Pelmatochromis* is closely related to, or even a member of the genus *Tilapia*.

Thys (1968a) expressed the view that *Pelmatochromis nigrofasciatus* (which he mistakenly identified as *P. ocellifer*; see Trewavas, 1973) and *Pterochromis congicus* (then included in *Pelmatochromis*) seemed to bridge the morphological gap between *Pelmatochromis* and *Tilapia*. He also included in that bridging group *Pelmatochromis ruweti*, a species now included, and properly so, in *Tilapia* (see Thys, 1968a). As a member of that genus, *T. ruweti* is excluded from the discussion which follows.

Reasons for considering *Pelmatochromis nigrofasciatus* and *Pterochromis congicus* being close to, or actually members of *Tilapia* are, according to Thys, the common possession of a *Tilapia*-spot

on the dorsal fin, the presence of microbranchiospines, lanceolate and not tuberculate gill-rakers, pointed pelvic fins in both sexes, 16 scales around the caudal peduncle, no hanging pad in the pharynx and '... all stages (with regards to mouth shape and dentition) of a gradual transition to *Tilapia sparrmanii*, type species of the genus *Tilapia* ...' (Thys, 1968a: 369).

Of the characters he lists, all but the dentition and gill-rakers in both *Pelmatochromis* and *Pterochromis*, and the oral ones in *Pterochromis*, are plesiomorphic features and thus of no value in establishing relationships.

Jaw morphology in all three species of *Pelmatochromis* is very close to that in *Tilapia sparrmanii* (and other *Tilapia* species) and therefore cannot be considered as bridging the gap between the *Tilapia* condition and the far more extreme, predator-like one characterizing *Pterochromis* (see p. 155). Nor can I agree with Thys' comment on the gill-rakers as applied to *Pelmatochromis*. As has been frequently mentioned in this paper, the gill-rakers in that genus closely resemble those in the chromidotilapiines, and are quite unlike the relatively simple, near-vertically orientated structures in *T. sparrmanii* and indeed of other *Tilapia* species (the concept of *Tilapia* used here being that of Trewavas, 1983). Admittedly there is some resemblance between the gill-rakers of *Pterochromis congicus* and those of certain tilapiine species, but there are no other features to suggest either a close relationship between that species and any *Tilapia* or any *Pelmatochromis* species (see above, pp. 155–6).

Thus, the only characters which might be of relevance are the dental ones. Since the teeth of *Pterochromis* are all unicuspid and conical, and bear no resemblance to those occurring as the principal dental elements in any *Tilapia* species (see Trewavas, 1973: 12), *Pterochromis* can be dismissed immediately from this aspect of the discussion.

Trewavas (1973) deals at length with the presumed resemblances between *Pelmatochromis* and *Tilapia* teeth. From her survey she concluded that 'The only species of *Pelmatochromis* showing any evidence of derivation from an ancestor with a *Tilapia*-like dentition is *P. nigrofasciatus*. The fact that the teeth are notched only at such an early stage that they can hardly be functional as such suggests that they are a vestigial feature derived from an ancestor that had indeed a *Tilapia*-like dentition' (*op. cit.*: 19).

Broadly speaking, I would agree with Trewavas' views on the teeth being a vestigial feature, especially since there are traces of a bicuspid juvenile dentition in another *Pelmatochromis* species (see p. 145). But even though, in the present state of our knowledge, *P. nigrofasciatus* has the most clearly bicuspid juvenile teeth, I would not consider them to be strictly *Tilapia*-like in detail. Rather, I would consider that they share with those of *Tilapia* only the feature of a bicuspid crown. The shared possession of teeth with bicuspid crowns, however, is too vague a character to use critically when attempting to unravel phyletic relationships, the more so since simple bicuspid crowns would seem to be a primitive adult condition amongst African cichlids (Greenwood, 1979; 1980), and there are many and derived variants on the bicuspid theme.

In short, none of the features listed by Thys (1968a) would support either a conclusion that *Pelmatochromis* and *Pterochromis* be treated as members of the genus *Tilapia*, or that the two taxa are closely related to *Tilapia* and might be derived from a *Tilapia busumana* or *T. buttkoferi*-like ancestor as was suggested by Thys (1968a: 377).

Thys' suggestions led me to check carefully on the published diagnostic features for *Tilapia* and to examine in some detail specimens of *T. busumana*, *T. sparrmanii*, *T. ruweti* and *T. zilli*. The object of that study was not only to see if there are synapomorphic features shared by *Tilapia* and *Pelmatochromis*, but to find autapomorphic features which would define *Tilapia* and the group tilapiini as a whole (*sensu* Trewavas, 1983). Neither search proved successful.

Trewavas' (1983) detailed account of *Tilapia* in relation to its sister taxa *Oreochromis*, *Sarotherodon* and *Danakilia* provided only one synapomorphic feature for those genera, namely a long gut. The other derived features apparent from her account are autapomorphies for the various genera other than *Tilapia*, which seemingly has no defining autapomorphies, at least in its morphological characteristics. My studies on the cranial and pharyngobranchial anatomy of *Tilapia* also failed to produce a single autapomorphy.

One feature not previously noted, however, would seem to provide an additional synapomorphy for the tilapiines as a whole. Namely, the shape, in lateral profile, of those pharyngeal teeth situated



Fig. 30 Two 'kukri' shaped lower pharyngeal teeth from the anterior dental field in *Oreochromis variabilis*. Magnification $\times 100$ (BMNH 1911.10.28:14).

in the anterior dental field of the lower pharyngeal bone. In the majority of cichlids, both African and Neotropical, these teeth are simple unicuspid or are clearly bicuspid. In either type, the tip of the cusp lies in the vertical passing through the body of the tooth or but slightly behind it. The tilapiines, however, have anterior field teeth with a very distinctive cusp form; the upper part of the tooth is angled posteriorly, and the vertical through its tip lies well behind the body of the tooth. When viewed laterally such teeth have an outline recalling the blade of a 'kukri', the Nepalese knife much favoured as a weapon by Gurkha soldiers (see Fig. 30). I have checked several species in each of Trewavas' (1983) tilapiine genera *Tilapia*, *Oreochromis*, *Sarotherodon*, and the monotypic *Danakilia* and *Iranocichla*, and find that 'kukri' teeth are present in all. Interestingly, none was recognizable in the endemic tilapiine genera of the Cameroonian lake Barombi Mbu (*Myaka*,

Konia, *Stomatepia* and *Pungu*), while in the Levantine *Tristramella*, teeth closely approaching the 'kukri' type are present, but apparently restricted to the posterolateral dental fields. 'Kukri' teeth do not occur in any of the pelmatochromine genera.

'Kukri'-shaped teeth, or teeth closely similar to them, also occur in at least some Lake Malawi species of the genus *Pseudotropheus*, for example, *P. tropheus*, *P. auritus* and *P. livingstoni* (not all species of this large genus were examined). That record, coupled with the general absence of 'kukri' teeth in other African and Neotropical taxa suggests that such teeth have evolved at least twice within the family since there is no evidence to suggest that *Pseudotropheus* and the tilapiines are closely related.

Another apomorphic feature in the pharyngeal jaws of all but one species of the *Tilapia*, *Oreochromis*, *Sarotherodon*, *Danakilia*, *Iranocichla* group, concerns the shape and spatial relationships of the upper pharyngeal bone (fused 3rd and 4th pharyngobranchials) of each side. Whereas in *Pelmatochromis*, *Pterochromis* and all the chromidotilapiines, as well as in the majority of African and Neotropical taxa, the two bones form a broad and shallow V (see p. 149, and Fig. 4A), in the tilapiine genera the bones are closely apposed along their medial faces, and together have a distinctly cardiform outline (Fig. 4B), one enhanced by their relatively broader and less ovoid toothed surfaces. The exceptional species is *Tilapia busumana*. Here the bones are narrower and form the generalized V-shape. *Tilapia busumana* is, of course, the species which Thys (1968a:377) indicated as being close to the stem of the pelmatochromine assemblage. Arguments for not accepting a close relationship between *Pelmatochromis* (or any pelmatochromine) and *Tilapia* have been given above, and are not affected by the two taxa sharing this plesiomorphic feature. That it is a plesiomorphy lost in, apparently, all other tilapiines, would, however, seem to indicate the possibility of *T. busumana* being a primitive tilapiine.

A cardiform arrangement of the upper pharyngeal bones is by no means confined to the tilapiine genera. It has been found in *Labrochromis* and *Astatoreochromis* from Lake Victoria, in *Tylochromis* and *Cardiopharynx* of Lake Tanganyika, in *Cyathochromis* and *Petrotilapia* from Lake Malawi, and in at least four Neotropical species as well. A condition approaching the cardiform one more closely than the V-shaped arrangement occurs in the supposedly primitive Asiatic *Etroplus oligacanthus* and in the Malagasian *Ptychochromis*. Arrangements intermediate between the cardiform and V-shaped types, but rather closer to the former, are found in *Simochromis* and *Xenotilapia* from Lake Tanganyika and *Paratilapia polleni* from Madagascar, and a reversed cardiform arrangement (with the 'auricular' part of the 'heart' directed anteriorly rather than towards the oesophagus) occurs in the Malagasian *Paretroplus dami*.

With such a range of variability, and of distantly related taxa in which the cardiform arrangement occurs, it would seem to be a feature which has evolved several times, and independently, within the Cichlidae, including some of its members generally accepted as having a plesiomorphic level of organization (e.g. *Tylochromis* and the etroplines of Asia and Madagascar). That it is an apomorphic feature seems probable from its absence in other labroids and in the percoid outgroups examined.

In the majority of species with a cardiform arrangement, the teeth of the upper pharyngeal bones are either enlarged and molariform, or fine, numerous and densely packed, a situation which may be correlated with the bones themselves having a larger surface area relative to the subvoid bones associated with the typical V-shaped arrangement.

The absence of 'kukri'-shaped teeth on the lower pharyngeal bones, and the persistence of the plesiomorphic V arrangement of the upper pharyngeal elements in all pelmatochromine taxa, provide yet other reasons for refuting the idea that *Pelmatochromis* and *Pterochromis* are members of the tribe Tilapiini *sensu* Trewavas (1983). That assemblage besides *Pelmatochromis* and *Pterochromis*, contains the genera *Tilapia*, *Oreochromis*, *Sarotherodon*, *Danakilia*, *Iranocichla*, *Tristramella*, the endemic genera of Barombi Mbu, and possibly *Steatocranus* and *Gobiochromis*. Its only unifying group-character cited is the *Tilapia*-type apophysis, which as Trewavas (*op. cit.* and 1986) recognises, is plesiomorphic for the cichlids. As such it cannot be used to establish the monophyly of the Tilapiini (see also Greenwood, 1978, and 1987).

Establishing the monophyly of Trewavas' Tilapiini, even after the removal of *Pelmatochromis* and *Pterochromis*, is a task that remains to be done. The use of upper pharyngeal bone arrange-

ment, and the presence of 'kukri'-shaped teeth may prove of some value in that task, but neither feature can yet be considered a fully corroborated synapomorphy for the group.

Of the two taxa which can be eliminated from the Tilapiini, *Pelmatochromis* may be the plesiomorph sister taxon to all the chromidotilapiines (see p. 192), but the relationships of *Pterochromis* are at present unknown (see p. 192). Its principal diagnostic phenotypic characters are all autapomorphic ones that could be derived, by differential growth, from a *Pelmatochromis*-like ancestor which did not have the derived gill-raker morphology of the extant *Pelmatochromis* species. Other changes from such a presumed ancestor would involve slight modifications to the dentation and dental patterns.

All that is speculation, and a reflection of the fact that such a proto-*Pelmatochromis* could well provide a morphotype from which a number of extant lineages, including *Tilapia* and its close relatives, evolved. If that is so, their unifying synapomorphies have still to be identified.

In conclusion, what can be said about the intrafamilial relationships of chromidotilapiines, *Pelmatochromis* and *Pterochromis*? In a positive sense, the answer must be 'Nothing'. Previously suggested relationships can be refuted, and one is left with a number of apparently monophyletic lineages whose relationships at higher phyletic levels are presently indeterminable.

The distribution of *Pterochromis*, *Pelmatochromis* and the chromidotilapiines

The chromidotilapiines as a whole (*Thysia*, *Chromidotilapia*, *Pelvicachromis*, *Limbochromis*, *Parananochromis* and *Nanochromis*) have a fairly extensive latitudinal range from about 10°N to 5°S. They are, however, with the exception of *Nanochromis* and one *Chromidotilapia* species, confined to a relatively narrow strip, some 200–300 miles wide, extending along the western margin of Africa. This strip lies mainly within the lowland forest zone, but in places it extends into the areas of moist woodlands and savannah. The range of *Nanochromis*, however, extends further eastwards into the central regions of the Zaire river and its tributaries, although the greater number of its species is found in the fast-flowing waters of the river's lower reaches. The exceptional *Chromidotilapia* species, *C. schoutedeni* occurs outside the marginal zone and is found in the lower parts of the Lualaba river.

Pelmatochromis has a wide but scattered distribution which includes the central Zaire area, Senegal, Guinea, Liberia and Sierra Leone, while *Pterochromis* is apparently restricted to Central Zaire in the region of Kisingani. For detailed distributions of the various species see Thys, 1968a; Thys & Loisel, 1971; Loisel & Welcomme, 1972; Trewavas, 1973 and 1974; Roberts & Stewart, 1976; Linke & Staech, 1981; Stewart & Roberts, 1984.

There is remarkably little distributional overlap between the chromidotilapiines, *Pelmatochromis* and *Pterochromis* on the one hand, and any of the non-tilapiine fluviatile species of eastern and middle Africa on the other. The non-tilapiine species in question are represented by members of the haplochromine genera *Astatotilapia*, *Ctenochromis*, *Thoracochromis*, *Astatoreochromis* and *Orthochromis* (see Greenwood, 1979).

In geographical terms, and to a certain extent in their trophic specializations as well, the chromidotilapiines, plus *Pelmatochromis* and *Pterochromis*, together with *Hemichromis* and *Anomalochromis* (see Greenwood, 1985a & b) seem to be the far western equivalents, and ecological counterparts, of the eastern haplochromines mentioned above. It is, of course, difficult to quantify degrees of morphological differentiation, but the two geographical entities seem to have evolved and differentiated to about the same extent. A noticeable difference, however, is the absence of any far western species in which the pharyngeal mill is hypertrophied. Indeed, the morphological details involved in the differentiation of the two groups are generally quite different. For example, no eastern species has evolved a dentition like that in the chromidotilapiines, none has a visor-like hanging pad in the pharynx, none has gill-rakers with the complex form of those in the chromidotilapiines, and all have retained microbranchiospines. However, in superficial features the eastern and western rheophilic taxa, *Orthochromis* and *Nanochromis* respectively, are, perhaps not unexpectedly, remarkably similar.

Summary and conclusions

The pelmatochromine cichlids (*sensu* Thys, 1968*a*) of western Africa can be divided into a monophyletic lineage (informally categorized as the chromidotilapiines) comprising the genera *Thysia*, *Chromidotilapia*, *Pelvicachromis*, *Nanochromis*, *Parananochromis* and *Limbochromis* (the two latter genera described in this paper), and two other monophyletic taxa, *Pelmatochromis* and *Pterochromis*.

The intrarelationships of the chromidotilapiines cannot be satisfactorily resolved; it is suggested that *Thysia* is the plesiomorphic sister taxon to the other five genera combined, and that within this combination *Parananochromis* and *Nanochromis* are sister genera, and are the most derived members of the chromidotilapiines.

There are indications that two of the chromidotilapiine genera, although monophyletic assemblages themselves, should be subdivided. In *Nanochromis*, for example, one group of species has the posterior half of the upper lateral-line in contact with the dorsal fin base, whilst in the other, only the last four or five scales of the lateral-line are contiguous with the fin base. In *Pelvicachromis*, *P. humilis* shows certain derived features which suggest that it may represent an off-shoot of the main species assemblage. Both these problems may be clarified when more material is available, and further anatomical and osteological studies can be made. Ethological and other aspects of the species' natural history may also prove of great value in unravelling the still outstanding problems.

Although *Pelmatochromis* apparently shares one derived character, the nature of its gill-rakers, with the chromidotilapiines, no further and congruent synapomorphies could be discovered to support its possible sister-group relationship with those species. Equally, the absence of other derived features in *Pelmatochromis* does not give any indication of other taxa to which it might be related.

Pterochromis exhibits several autapomorphic features but, like *Pelmatochromis*, it seems to show no derived features positively indicative of its relationships within the family.

The suggestion (Thys, 1968*a* & *b*) that *Pelmatochromis* might be closely related to, or even a member of the genus *Tilapia* is reexamined and found to be untenable both for the reasons given by Trewavas (1973) and on the basis of other characters as well. Its suggested membership of a tribe containing *Tilapia*, *Oreochromis*, *Sarotherodon* and several other genera (see Trewavas, 1983) is also rejected. In that connection, the phylogenetic basis (as opposed to one based on overall similarity) of the Tilapiini is reconsidered. Two possibly apomorphic characters, for at least some members of the tribe, are identified; neither is present in any of the pelmatochromine taxa, thus providing further evidence against their possible close relationship with *Tilapia*.

Neither the chromidotilapiines nor *Pelmatochromis* and *Pterochromis* are closely related to any of the fluviatile haplochromine lineages from eastern Africa, and there is very little geographical overlap between the two groups. The essentially far western distribution of the chromidotilapiines, *Pelmatochromis* and *Pterochromis* contrasts strongly with the wider geographical distribution of the eastern haplochromine lineages (see above, p. 199, and Greenwood, 1979).

Like the various haplochromine lineages of Lake Victoria (see Greenwood, 1981; 1984), the chromidotilapiines exhibit a gradual trend in the evolution of certain morphological characters, with each stage in the morphocline represented by one or several species. Amongst the Lake Victoria haplochromines this display of cladistic gradualism principally involves trophic specialization. In the chromidotilapiines it involves traits associated with an increasingly rheophilic way of life. Little is known about the feeding habits of the chromidotilapiines but judging from the oral and pharyngeal dentition, and from associated structures, there is probably little intragroup trophic specialization and differentiation.

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